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CONTENTS

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ENERGY REQUIREMENTS OF ADULT CAPE VULTURES (*Gyps coprotheres*)

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ABSTRACT.—Outdoor feeding trials were used to determine gross energy intake, energy assimilation efficiency and metabolizable energy intake of captive adult Cape Vultures (*Gyps coprotheres*). The mean ash-free dry energy density of daily pooled samples of feces and urine was 14.0 ± 0.2 kJ/g. A consistently high mean energy assimilation efficiency of 86.2 ± 2.7% caused daily energy content of excreta to fluctuate according to the quantity of energy assimilated. Mean gross energy intake was 2926.8 ± 349.1 kJ/day and mean metabolizable energy intake was 2552.9 ± 300.9 kJ/day for birds with changes in body mass of 2% or less between start and end of feeding trials. The daily energy expenditure of a free-living adult, weighing 8.3 kg, was estimated to be 3006 kJ/day (DEE = 826.7 kJ/day × $kg^{0.61}$).

Requerimientos de energía del buitre de la especie *Gyps coprotheres*

EXTRACTO.—Experimentos de alimentación al aire libre, con buitres de la especie *Gyps coprotheres* en cautividad, fueron realizados para determinar: la cantidad total de energía ingerida en el alimento; la eficiencia en la asimilación de esa energía; y la cantidad de energía ingerida y disponible para el metabolismo. La media de la energía, libre de carbón de todas las muestras diarias de la combinación de heces y orina, fue de 14.0 ± 0.2 kJ/g. La media de la eficiencia de asimilación de energía, que fue consistentemente alta: 86.2 ± 2.7%, causó que el contenido de energía excretada por día fluctuara de acuerdo con la cantidad de energía asimilada. La media de la energía total ingerida fue 2926.8 ± 349.1 kJ/día; y la media de la energía ingerida y disponible para el metabolismo fue 2552.9 ± 300.9 kJ/día, para aves con cambios en la masa corporal de 2% ó menos, entre el comienzo y el fin del experimento. El gasto diario de energía de un adulto que vive en libertad, y que pesa 8.3 kg, se estimó en 3006 kJ/día (GDE = 826.7 kJ/día × $kg^{0.61}$).

[Traducción de Eudoxio Paredes-Ruiz]

Vultures include some of the heaviest raptorial birds, yet constitute a poorly studied group in bioenergetics research (Komen 1991). Intrinsically difficult to study in the field, bioenergetic research of vultures has only been done under captive conditions, and has mostly been limited to measurements of gross food intake for a few vulture species (Jarvis et al. 1974, Hiraldo 1976, 1983, Houston 1976, Mendelssohn and Leshem 1983, Komen 1991).

Like their congeners elsewhere, Cape Vultures (*Gyps coprotheres*) are scavengers of ungulate carcasses, and, in rural areas which no longer support wild ungulate herbs, scavenge domestic livestock (Mundy 1982, Robertson and Boshoff 1986). Foraging success of adult Cape Vulures is dictated by unpredictable food resources and climatic conditions (Boshoff et al. 1984, Robertson and Boshoff 1986), and, while rearing nestlings, vultures may only forage once every two days (Komen 1991). If we assume that the maximum food intake of Cape Vultures is dictated by stomach and crop capacity (Komen 1986), measurements of daily metabolizable energy intake for existence, and estimates of daily energy expenditure in this study, provide an indication of energetic constraints on these large raptorial birds while breeding.

METHODS

Ten adult Cape Vultures were maintained in captivity at the De Wildt Raptor Research Centre (25°41'S 27°56'E), Transvaal, South Africa. For the purpose of this study an "adult" vulture is defined as a full-grown vulture which is one year old or older, and falls within the normal range of adult body mass and standard wing-length (Mundy 1982, Komen 1986).

Table 1. Water, lipid, protein, ash and carbohydrate content, and energy density in kJ/g (Ash-free dry (AFD) and wet) of different meat types consumed by adult Cape Vultures during three feeding trial periods.

Trial Period and Food-Type	Percent					Energy Density	
	Water	Lipid	Protein	Ash	Carbohydrate	kJ/g AFD	kJ/g Wet
1 (Horse)	71.2	1.7	22.0	3.4	1.8	25.1	6.4
2 (Cow 1)	72.5	2.4	21.7	2.8	0.6	27.0	6.7
3 (Cow 2)	69.7	1.9	19.2	8.7	0.5	26.0	5.6
Mean	71.1	2.0	21.0	5.0	1.0	26.0	6.2
±SE	1.4	0.4	1.5	3.3	0.7	1.0	0.6
CV[1]	2.0	20.0	7.1	66.0	70.0	3.9	9.7

[1] CV = Coefficient of variation.

Of the ten vultures, three, five, and seven vultures were used in three feeding trial sessions, for a total of 15 feeding trials, with some of the vultures used in more than one trial. Trial vultures were removed from their flight aviary, weighed and placed in trial-cages on the same day at the start of the acclimation period of a particular feeding trial session. During these outdoor feeding trials, the vultures were maintained separately in visually-isolated cages (2 × 1.5 × 1 m), large enough to allow the birds to turn around and extend their wings fully. Each cage had a wire-mesh floor under which a removeable plastic-lined tray was placed to facilitate the collection of excreta. During the feeding trials, monthly minimum temperatures ranged between 3–8°C during June through September (trial sessions 1 and 2) and 14–17°C during October and November (trial session 3). Maximum monthly temperatures were 21–25°C during July through September and 26–33°C during October and November. Ambient temperature did not appear to have an effect on food intake (see results).

Energy requirements for maintenance (gross energy intake and metabolizable energy) were determined by the food consumption method (Gessaman 1973). Each vulture was allowed to acclimatize for a few days preceeding the trial. During this acclimation period the birds were fed to satiation and provided free drinking water. Depending on how quickly each individual settled down behaviorally (e.g., cessation of restlessness and acceptance of hand-fed meat), a vulture's pre-feeding starvation period would be initiated. This period lasted between 2–4 d to ensure a post-absorptive state. Food was first offered on the morning when the most recently voided excreta no longer had a visible black fecal fraction; this suggested that all meat last consumed (from two to four days previously) had been assimilated and excreted. At this stage of starvation the white urinary fraction had a green tinge in most individuals.

On the first day of feeding birds mostly ate to satiation (in excess of 1.0 kg meat). Thereafter food intake decreased to almost negligible amounts after 4–5 d of feeding (pers. observations). Accordingly, the number of days on which food was offered was dictated by individual demand; a feeding trial was ended when a bird no longer demanded food.

To measure existence metabolism which requires the maintenance of "constant" body mass (i.e., 2% or less change in body mass between the start and end of a trial), feeding trials included post-feeding starvation periods lasting as long as 5 d, depending on the body mass of a bird on the morning after the day of last feeding. The 15 trials (including pre- and post-feeding starvation periods) therefore lasted between 12 and 18 d, with periods of actual feeding ranging from 6–11 d.

Each bird was weighed at least four times during a feeding trial: prior to the pre-feeding starvation period, prior to the feeding period, after the feeding period, and at the end of the post-feeding starvation period. Water was not offered at any stage of the feeding trial. The vultures were fed lean cow or horse meat obtained from livestock carcasses. Their diet was supplemented with a mineral-vitamin mixture (Beefee, Centaur Co., Johannesburg, South Africa). Three different types of meat were used in the trials. Meat was deep frozen in labeled plastic bags, and on the evening prior to the next morning's feeding bags were removed and defrosted. Care was taken to give all trial birds the same type of meat on a given day of feeding. The same three types of meat were available for all three feeding trial sessions. On feeding days, each bird was fed once by hand to satiation, and food intake was determined by weighing meat before feeding and leftovers immediately after feeding. Spilled food and regurgitations were collected whenever these occurred. Regurgitations were oven-dried at 60°C to constant mass. The dry mass of a regurgitation was subtracted from the calculated dry mass of food consumed on the same day the regurgitation occurred.

Five samples (100 g each) of each meat type (Table 1) used for a feeding trial were taken for analyses. Each sample was oven-dried at 60°C to constant mass. Water loss was calculated by subtraction, and mean water content calculated for the five samples. The dried samples were pooled, ground to a powder and analysed for energy density (Gallenkamp ballistic bomb calorimeter) and inorganic content by ashing (see Komen 1986, 1991 for details). Metabolizable energy and assimilation efficiency of birds in any one trial period were calculated using the mean composition data for all meat types consumed during that trial. The mean "wet" energy density of all meat types consumed was 6.2 kJ/g (SE ± 0 6 kJ/g, range 5.6–6.7 kJ/g; Table 1).

All feces and urine (hereafter referred to as excreta) were collected from each bird twice daily, for each day after the initiation of feeding until the end of post-feeding starvation period (i.e., when a black fecal fraction was no longer present in excreta) and pooled. These daily quantities of excreta from each bird were oven-dried at 60°C to constant mass and weighed separately. They were then analysed for energy density and inorganic content (see Komen 1986 for details). To determine assimilation efficiency the daily excreta weights were pooled for each trial. Twenty-three day-samples were randomly selected from all individual day-samples ($N = 186$) collected during the three feeding trial sessions and analysed for energy density (kJ/g ash-free dry mass) and ash content.

The efficiency with which birds assimilate energy was determined following Gessaman (1973):

$$ME = GEI - (F + U)$$

Table 2. Changes in body mass during 15 feeding trials of 10 Cape Vultures (A–J), showing percentage change between the pre-feeding and post-trial body masses.

Trial Period and Bird	Duration of Trial[1] in Days	Body Mass (g)						
		Pre-Trial	Pre-Feeding (A)	Post-Feeding	Post-Trial (B)	Mean	±SE	% Change (B − A)/A•100
1 A	15 (12)	9150.0	8800.0	9220.0	8840.0	9002.5	184.7	0.5
B	17 (14)	9580.0	9200.0	10 080.0	9445.0	9576.3	321.2	2.7
C	14 (11)	9600.0	9250.0	9455.0	9200.0	9376.3	160.7	0.5
2 D	17 (14)	7100.0	6720.0	7165.0	6785.0	6942.5	192.8	1.0
E	17 (14)	7620.0	7220.0	7615.0	7225.0	7420.0	197.5	0.1
F	12 (9)	8050.0	7720.0	7715.0	7715.0	7800.0	144.4	−0.1
G	13 (10)	8150.0	7770.0	7465.0	7465.0	7712.5	281.6	−3.9
B	18 (15)	9070.0	8670.0	10 665.0	9630.0	9508.8	749.6	11.1
3 D	15 (12)	7550.0	7170.0	7675.0	7140.0	7383.8	233.2	−0.4
E	17 (13)	7740.0	7370.0	8275.0	7640.0	7756.3	328.7	3.7
F	17 (13)	7445.0	7070.0	7975.0	7350.0	7460.0	327.7	4.0
G	17 (13)	6650.0	6270.0	7225.0	6585.0	6682.5	344.6	5.0
H	17 (13)	7575.0	7170.0	7975.0	7300.0	7505.0	308.2	1.8
I	14 (11)	6860.0	6470.0	7175.0	6550.0	6763.8	278.6	1.2
J	15 (12)	6825.0	6470.0	7275.0	6600.0	6792.5	306.2	2.0
Mean		7931.0	7556.0	8197.0	7698.0	7845.5		1.9
±SE		955.4	960.1	1084.9	1026.7	985.8		3.2

[1] First numeral represents duration of each trial, numeral in brackets represents number of days between pre-feeding and post-trial weighings.

where ME = metabolizable energy, GEI = gross energy content of food consumed, F = energy content of feces and U = energy content of urine; and assimilation efficiency (AE):

$$AE = 100 \times \{GEI \pm (F + U)\}/GEI[\%]$$

Results

The mean change in individual adults' pre-feeding and post-trial body masses was 1.9% (SE ± 3.2%, range 0.1–11.1%, N = 15 trials) and the majority of birds gained body mass during the trials (Table 2). During 10 of the 15 trials, the vultures had body mass changes of about 3% or less, and of the remaining trials, only one bird had a marked decrease (−3.9%) in body mass, the rest (N = 4) had body mass increases ranging between 3.7% and 11.1%. Mean pre-feeding body mass of all birds was 7556.0 g (SE ± 960.1 g, range 6270–9250 g) and mean post-trial body mass was 7698.0 g (SE ± 1026.7 g, range 6550–9630 g).

There was considerable variation in individual gross daily food intake (Table 3). Mean daily gross food intake was 479.2 g meat/day (SE ± 52.9 g meat/day, range 372.6–558.7 g meat/day), and represents 6.5% of body mass (SE ± 1.3%, range 4.0–8.4%; Table 3).

Gross energy content of the daily excreta of individual birds changed proportionally to the energy content of food consumed. The mean ash-free dry (AFD) energy density of daily excreta was 14.0 kJ/g AFD (SE ± 0.2 kJ/g AFD, N = 23 individual daily samples analysed, range 13.9–14.1 kJ/g AFD). The mean inorganic content of these excreta samples was 7.1% (SE ± 0.2%, N = 23, range 6.9–7.2%).

There was no significant difference between mean gross energy intake of each trial session (ANOVA, F = 3.29, df = 2, 12, $P > 0.05$), and the results for all three trial sessions were combined. Mean daily gross energy intake for all birds was 2926.8 kJ/day (SE ± 349.1 kJ/day, N = 15 trials, range 2347.5–3743.3 kJ/day). Gross energy assimilation efficiency was consistently high at 86.2% (SE ± 2.7%, range 83.2–88.2%) and mean daily metabolizable energy was 2522.9 kJ/day (SE ± 300.9 kJ/day, range 2023.6–3226.7 kJ/day, N = 15 trials).

Existence metabolism, which is equivalent to metabolisable energy providing the birds undergo body mass changes of about 2% or less between the start and end of a trial (*sensu* Gessaman 1973), was 2420.3 kJ/day (SE ± 93.2, N = 9 trials).

Table 3. Gross food intake (g meat/day and % of pre-feeding body mass (BM)), and daily energy requirements (kJ/day, gross energy intake (GEI) and metabolizable energy (ME)) of ten captive adult Cape Vultures (A–J) calculated for the number of days between pre-feeding and post-trial weighings (see Table 2) during feeding trials.

TRIAL PERIOD AND BIRD	TOTAL MEAT CON-SUMED g	MEAT/DAY g/day	% OF BM %	DAILY GEI kJ/day	DAILY ME[1] kJ/day
1 A	5005.0	417.1	4.7	2669.4	2301.0
B	6735.0	481.1	5.2	3079.0	2654.1
C	4099.0	372.6	4.0	2384.6	2055.5
2 D	6965.0	497.5	7.4	3333.3	2873.3
E	5904.0	421.7	5.8	2825.4	2435.5
F	4145.0	460.6	6.0	3086.0	2660.1
G	4531.0	453.1	5.8	3035.8	2616.9
B	8380.0	558.7	6.4	3743.3	3226.7
3 D	5020.0	419.2	5.8	2347.5	2023.6
E	6615.0	508.8	6.9	2849.3	2456.1
F	7145.0	549.6	7.8	3077.8	2653.1
G	6610.0	508.5	8.1	2847.6	2454.6
H	6220.0	478.5	6.7	2679.6	2309.8
I	5960.0	541.8	8.4	3034.1	2615.4
J	6235.0	519.6	8.0	2909.8	2508.3
Mean	5971.3	479.2	6.5	2926.8	2522.9
±SE	1168.0	52.9	1.3	349.1	300.9

[1] ME calculated using mean energy assimilation efficiency of 86.2%.

DISCUSSION

Cape Vultures are relatively inactive raptors; soaring flight presumably allows them to forage in an energetically inexpensive fashion (Pennycuick 1972), and they spend a major part of each day roosting (Mundy 1982, Boshoff et al. 1984, Robertson and Boshoff 1986). Taking advantage of prevailing climatic conditions, wind and thermals, Cape Vultures in summer rainfall areas of southern Africa generally leave their colonial roosts to forage from early to mid-morning and return in the afternoon, generally precluding more than one foraging trip per day (Brown 1988, J. Komen unpubl.). While rearing young, each parent may therefore only forage once every 2 d (Komen 1991). Cape Vultures have been reported to forage as little as once every 3 d (Robertson and Boshoff 1986) and during the post-fledging dependency, young birds may go without food for much longer periods (up to 16 d; Robertson 1985).

The results of adult Cape Vulture feeding trials in captivity provide data on gross energy intake and metabolizable energy which probably represent minimum requirements for existence, taking into account the relative inactivity of both free-living vultures and captive birds. Starved Cape Vultures can consume 1.5 kg meat in one feeding (Komen 1991). This equivalent to a gross energy intake of 9300 kJ, which, with a high assimilation efficiency (86.2%), represents a maximum metabolizable energy intake of 8017 kJ. Kirkwood (1980) predicted that the mean maximum daily metabolizable energy intake by any animal is 1713 kJ/day × $kg^{0.72}$ (SE of slope ± 0.008). Using Kirkwood's (1980) equation, the predicted maximum daily metabolizable energy intake for Cape Vultures ranges between 6409 and 8499 kJ/day (using the lowest and highest post-starvation body masses in this study; Table 2). Starved, low weight, adult Cape Vultures therefore appear to exceed the theoretical maximum for daily metabolizable energy intake, by being able to consume a single large quantity of food which provides metabolizable energy for more than one day of existence. This suggests a strategy to counter unpredictable food resource and extended periods of inclement weather.

Daily energy expenditure is estimated to be about 1.2 times existence metabolism in small, non-breeding (and thus relatively inactive), diurnal raptors (Sapsford and Mendelsohn 1984). Since metabolism does not scale in direct proportion to body mass, birds with large bodies would have relatively lower metabolic rates than birds with small bodies (Lasiewski and Dawson 1967, Walsberg 1980). Accordingly, daily energy expenditure of free-living Cape Vultures is probably not greatly elevated above existence metabolism, especially since they are inactive for a major part of each day, with little seasonal variability in this behavior.

The captive adults in this study were generally less massive than free-living adults, and assuming that energy requirements for existence are scaled to body mass regardless of differences in body constituent proportions, the energy requirements of free-living adults will be proportionally higher than that of captive adults. If existence metabolism and daily energy expenditure are scaled on body mass according to an exponent of 0.61 (Walsberg 1980), I estimate that daily existence metabolism of free-living adults is 2505 kJ/day (688.9 kJ/day × $kg^{0.61}$) for body mass equal to 8300 g (mean body mass 8298.3, SE ± 477.8 g, 11 wild adults weighed; Komen 1986), and daily energy expenditure (1.2 times existence metabolism) is 3006 kJ/day or 826.7 kJ/day × $kg^{0.61}$. This relatively low predicted value for daily energy expenditure is supported by

evidence from field and captive studies on diurnal and nocturnal raptorial birds (Koplin et al. 1980, Sapsford and Mendelsohn 1984, Wijnandt 1984, see also Walsberg 1980).

A single maximal feeding (9300 kJ) should theoretically provide enough energy to maintain an adult Cape Vulture for about 3 d, without expending body fat reserves. Fat content of free ranging adult Cape Vultures ranges between 9.5–15.7% of body mass, accounting for a fat depot of as much as 1346 g (Komen 1991). Assuming that stored fat has an energy density of 38 kJ/g AFD (Johnston 1970), and that 98% may be re-absorbed for metabolism, to the point where body condition is still "reversible" in the sense that an individual may be re-fed and thus survive the fast (Robin et al. 1988), then this fat reserve could theoretically maintain an adult bird during periods of food deprivation (assuming daily extence metabolism of 2505 kJ/day) for as long as 20 d, and probably longer if metabolic rate diminishes during fasting.

While rearing young, each parent should optimally be able to provide enough food on 1 d of every 2-d foraging cycle to satisfy the gross energy requirements of the nestling, for the duration of the nestling period of 136 d (Komen 1986, 1991). Daily gross energy intake of the growing nestling increases with age, and, during the period of maximum growth (about 40 d, or 20 parent foraging cycles), may be twice as much as the daily adult energy requirement for existence (Komen 1991, in preparation). However, at no stage does daily nestling gross energy intake exceed the maximum quantity set by adult crop and stomach capacity. Except during unusual periods of food deprivation, resulting from inclement weather conditions (Komen 1986, in preparation), both adult and nestling energy requirements should be satisfied, without undue demands on body fat reserves.

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ORGANOCHLORINES AND MERCURY IN OSPREY EGGS FROM THE EASTERN UNITED STATES

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Abstract.—Organochlorine and mercury concentrations were determined in Osprey eggs collected from Maryland, Virginia, and Massachusetts during 1986-87. DDE concentrations were significantly different among locations. Median DDE concentrations did not decline significantly in eggs from Glenn L. Martin National Wildlife Refuge, Maryland, between 1973 and 1986. The median DDE residue for eggs from Martin Refuge in 1986 surpassed the value associated with 10% eggshell thinning, but was below the value associated with production of 1.0 young per active nest, a level assumed to represent a stable population. DDD, DDT, dieldrin, PCB, and mercury residues in all eggs appeared insignificant with regard to potential effects on shell thickness or reproduction. DDE and PCB residues were lower in eggs collected in 1986-87 than in those collected in the 1970s for each area. DDD, DDT, and dieldrin were not detected in Martin Refuge eggs in 1986, representing a significant reduction since 1973. DDD, DDT, and dieldrin levels in Massachusetts and Virginia eggs in 1986-87 were similar to those in eggs from the 1970s for each state. Mercury residues in eggs from Martin Refuge may be increasing and although not significant in this study, may warrant future monitoring.

Mercurio y compuestos organoclorados en huevos de Águila Pescadora del este de los Estados Unidos

Extracto.—Concentraciones de mercurio, y compuestos organoclorados normalmente usados en pesticidas, fueron determinadas en huevos de águilas de la especie *Pandion haliaetus* colectados en Maryland, Virginia y Massachusetts durante 1986-87. Las concentraciones de DDE fueron significativamente diferentes de un lugar a otro. La media de las concentraciones de DDE no declinó significativamente en huevos colectados en el Refugio Nacional de Vida Silvestre Glenn L. Martin, Maryland, entre 1973 y 1986. La media de residuos de DDE, en huevos del Refugio Martin en 1986, sobrepasó el valor asociado con el 10% de disminución en el espesor de la cáscara; pero estuvo por debajo del valor asociado con la producción de una cría por nido activo, lo que es un nivel que se asume representa una población estable. Los residuos de DDD, DDT, dieldrine, bifenil policlorinado (PCB), y mercurio en todos los huevos parecían tener insignificantes potenciales efectos en el grosor de la cásara o en la reproducción. Los residuos de DDE y PCB en huevos colectados en 1986-87, fueron más bajos que los de aquellos colectados en los años 70 en cada área. DDD, DDT y dieldrine no fueron detectados en huevos del Refugio Martin en 1986, lo que representa una significativa reducción desde 1973. Los niveles de DDD, DDT y dieldrine en huevos colectados en Massachusetts y Virginia en 1986-87, fueron similares a aquellos de los colectados en los años 70 en cada estado. Puede que haya un incremento en los residuos de mercurio en huevos procedentes del Refugio Martin; y aunque no haya sido significativo para este estudio, puede que justifique futuros controles.

[Traducción de Eudoxio Paredes-Ruiz]

Osprey populations in the eastern United States, including Chesapeake Bay, began to decline in the late 1950s, continuing through the 1970s (Ames 1966, Schmid 1966, Henny 1977, Reese 1977). During this period, high concentrations of organochlorines, including DDE, dieldrin, and polychlorinated biphenyls (PCBs), were found in eggs of populations

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with poor reproductive success (Wiemeyer et al. 1975, Wiemeyer et al. 1978, Spitzer et al. 1978, Wiemeyer et al. 1988). By the early 1970s, productivity began to increase and continued through the 1970s in many portions of the Chesapeake Bay (Reese 1975, 1977). Also, preliminary data showed a decline in organochlorine levels found in Chesapeake Bay Ospreys in 1975–82 compared to 1971–73 (Wiemeyer et al. 1987). However, Osprey nestlings in areas such as Poplar Island, Tilghman Island, Glenn L. Martin National Wildlife Refuge and the mouth of the Choptank River, Maryland, have had decreased survival with mortality rates ranging as high as 40–75% (P.R. Spitzer unpubl.).

One possible cause of these isolated declines in nestling survival is contaminant accumulation in eggs or young. We present data on contaminants in Osprey eggs collected in 1986 from Martin Refuge, which supports one of the largest Osprey concentrations on the east coast. This area represents an Osprey "colony" where the cause of recent decreased nestling survival is unknown. Data on contaminants in Osprey eggs from the eastern United States collected in 1986–87 and Martin Refuge in 1973 are also presented. Our objective was to determine if concentrations of contaminants found in Osprey eggs from the eastern United States were at levels associated with adverse effects to reproduction, including nestling survival.

MATERIALS AND METHODS

Martin Refuge is located on the northern end of Smith Island, Somerset County, Maryland, and is bordered to the west by Chesapeake Bay, to the north by Kedges Straits, and to the east by Tangier Sound. Five freshly laid Osprey eggs were collected from randomly selected active nests in the spring of 1986. The eggs were double wrapped in aluminum foil, placed in plastic bags, and refrigerated soon after collection. Eggs were prepared for analysis in cooperation with staff of the Patuxent Analytical Control Facility of the U.S. Fish and Wildlife Service. The contents of each egg were emptied into separate chemically cleaned jars. Addled eggs collected from coastal Massachusetts (between Narragansett Bay and Buzzards Bay), and Virginia (York River area, Mobjack Bay, and Rappahannock River) as part of the 1986–87 U.S. Fish and Wildlife Service's "Northeast Bird Egg and Tissue Project" were prepared for analyses in a similar manner as Martin Refuge eggs collected in 1986. Field collection techniques and contaminant analyses for Osprey eggs collected at Martin Refuge in 1973 were described by Wiemeyer et al. (1988).

Eggs collected in 1986–87 were analyzed by laboratories under contracts administered by the Patuxent Analytical Control Facility, Laurel, Maryland, which monitored performance and assured quality. Organochlorines were analyzed by Weyerhaeuser Analytical and Testing Services, Tacoma, Washington. Briefly, portions of homogenized samples were mixed with sodium sulfate and extracted for 20 hr with petroleum ether. Lipid cleanup of extracts was by gel permeation chromatography. Analysis was conducted with a Hewlett Packard 5880A gas chromatograph with dual columns (DB1 and DB 1701) and dual electron capture detectors. Lower limits of detection, before corrections for dehydration, that varied among samples were <0.1 ppm for pesticides and PCBs, except for PCBs in Maryland eggs where the limit was ≤ 0.6 ppm. In addition to the contaminants reported here, the samples were also analyzed for chlordane isomers and metabolites, heptachlor epoxide, endrin, hexachlorobenzene, mirex, and several other compounds, none of which were detected. The Osprey eggs were analyzed in a batch process with other lots. The batch size for soxhlet extraction was 12 (11 samples and 1 blank). No analytes were detected in the blank at concentrations greater than 0.5 ppb. Duplicate analysis of one of the Martin Refuge eggs collected in 1986 resulted in standard deviations of 0.21 and 0.13 for DDE and PCBs, respectively. Duplicate analysis of one of the Northeast Egg and Tissue Project eggs resulted in standard deviations of 0.19, 0.12, 0.12, 0.05, and 0.50 for DDE, DDD, DDT, dieldrin and PCBs, respectively. Mercury was analyzed by Environmental Trace Substances Research Center, Columbia, Missouri, using cold vapor atomic absorption with a Perkin Elmer Model 403 AA. The limit of detection for mercury was 0.02 ppm. Duplicate analysis of a Martin Refuge egg collected in 1986 and a Northeast Egg and Tissue Project egg resulted in standard deviations of 0.07 and 0.04, respectively. Spike recoveries of individual eggs were 97% for eggs collected at Martin Refuge in 1986 and 107% for eggs collected for the Northeast Egg and Tissue Project. Eggshell thickness was not measured in eggs collected in 1986–87.

The volume of all eggs was measured by water displacement or estimated as described by Stickel et al. (1973). Contaminant concentrations were adjusted by egg wet weight to volume ratios (ppm) assuming a specific gravity of 1.0 (Stickel et al. 1966). To aid in quantitative data analyses, 0.05 ppm was used for eggs where a particular contaminant was not detected. However, when a contaminant was not found in any eggs for a particular location, residue levels were simply listed as "not detected."

Due to small sample sizes and uncertainty regarding the sampling distribution associated with our egg contaminant data, nonparametric statistical tests were used to differentiate between and among median contaminant concentrations. While median values and geometric means reported elsewhere in the literature are not directly comparable, both are valid measures of central tendency for a data set. Kruskal-Wallis tests (Chi-square approximation) were used to determine if differences existed among all locations with data on a particular contaminant (Sokal and Rohlf 1981). If significant differences in median values were found among locations, all pairwise multiple comparisons were made using Wilcoxon's signed-rank test for unpaired data (normal approximation, Sokal and Rohlf 1981). Statistical significance was assumed at $P < 0.05$, and Bonferroni's multiple comparison technique was used

Table 1. Median (and range) contaminant concentrations (ppm fresh wet weight) in Osprey eggs from several locations in the eastern U.S., 1973–87.

Location and Collection Year	Contaminant						
	N	DDE	DDD	DDT	Dieldrin	PCB	Mercury[a]
Maryland							
Glenn L. Martin NWR, 1973	11	3.4 (1.3–5.9)	0.44 (0.27–1.3)	0.14 (n.d.[b]–1.2)	0.05 (n.d.–0.20)	2.8 (1.8–4.3)	0.05 (0.03–0.11)
Glenn L. Martin NWR, 1986	5	2.3 (0.82–3.0)	n.d.	n.d.	n.d.	1.0 (0.59–2.3)	0.11 (0.70–0.24)
Virginia							
York River area, Mobjack Bay and Rappahannock River, 1987	5	0.65 (0.38–0.83)	0.05 (0.04–0.11)	0.13 (0.11–0.80)	0.01 (0.01–0.02)	3.7 (2.2–5.7)	0.11 (0.05–0.21)
Massachusetts							
Between Narragansett Bay and Buzzards Bay, 1986	4	0.56 (0.45–0.68)	0.13 (0.10–0.18)	0.23 (0.12–0.29)	0.03 (0.0[c]–0.04)	2.4 (2.16–2.50)	0.06 (0.05–0.23)

[a] Sample size for mercury analysis was five for Glenn L. Martin National Wildlife Refuge in 1973 and three for Massachusetts in 1986

[b] n d. = not detected.

[c] Actual value calculated as 0.001 but reported as 0.00 when rounded for consistency.

to control the Type I error rate at 0.05 (Miller 1981). All data analyses were performed using the PC version of SAS (SAS Institute, Inc. 1985). Statistical differences found between 1973 and 1986–87 data should be viewed with caution based on variations in chemical analytical techniques and laboratories used for these two separate data sets.

Results and Discussion

Median contaminant concentrations and range (ppm) in Osprey eggs from each area and year are given in Table 1. Residues of DDE were detected in all eggs from all locations and collection periods. Median concentrations of DDE did not decline significantly in eggs from Martin Refuge between 1973 and 1986 ($Z = 1.47$, $P = 0.14$). However, DDE concentrations were significantly different among locations sampled in 1986–87 ($\chi^2 = 8.52$, df = 2, $P = 0.014$). Multiple comparisons did not reveal statistically significant differences between location pairs, although eggs from Martin Refuge appeared to contain higher DDE residues than those from either Virginia ($P = 0.06$) or Massachusetts ($P = 0.06$). Eggs from similar areas of Virginia collected in 1976–77 contained geometric mean DDE concentrations of 1.8 to 2.6 ppm with the lowest concentration being 0.92 ppm (Wiemeyer et al. 1988). Eggs from the Westport River, Massachusetts in 1972–73, an area within the region sampled in 1986, had a geometric mean of 4.2 ppm DDE, with the lowest concentration being 2.0 ppm (Wiemeyer et al. 1988).

DDE residues have been clearly associated with adverse effects on Ospreys including decreased reproductive success and associated population declines, whereas other organochlorine pesticides have not been associated with such effects (Wiemeyer et al. 1988). Median values for DDE reported from Virginia and Massachusetts in 1986–87 were well below reported values associated with biologically significant effects on eggshell thickness and reproductive success (Wiemeyer et al. 1975, 1988). The median residue for DDE from Martin Refuge in 1986 surpasses the 2.0 ppm DDE concentration associated with 10% eggshell thinning but is well below the 4.2 ppm DDE associated with 15% eggshell thinning (Wiemeyer et al. 1988). Also, the median residue value for Martin Refuge in 1986 is less than the 2.6 ppm DDE value associated with a production rate of 1.0 young per active nest and assumed to represent a healthy and stable population (Wiemeyer et al. 1988). A production rate of 0.8 young per active nest is considered necessary to maintain a stable population (Spitzer et al. 1983). Eggs collected at Martin Refuge in 1973 contained higher median DDE residues (3.4 ppm); eggshell thinning was 17% (Wiemeyer et al. 1988) and young produced was about 1.5 per active nest (S.N. Wiemeyer

unpubl.) which was considered excellent. Wiemeyer et al. (1988) had predicted these egg residues to be associated with about 14% thinning and a production rate of about 0.9 young per active nest. The equation estimating the relationship between DDE concentrations and brood size for eggs collected after failure to hatch, gave production estimates that were below actual levels of production in nearly all sampled populations (Wiemeyer et al. 1988) and should be used with caution.

Residues of DDD, DDT, and dieldrin were not detected in any eggs from Martin Refuge in 1986; therefore, this location and colletion period was assumed to have the lowest concentration of these contaminants and data analyses include only the other locations. The median concentration of DDD plus DDT was significantly higher in eggs from Massachusetts than in those from Virginia ($Z = 2.08$, $P = 0.037$). DDD and DDT residues were combined in the statistical analysis because DDT is metabolized to DDD during embryonic development (Abou-Donia and Menzel 1968) and reductive dechlorination occurs in embryonated eggs following death (Walker and Jefferies 1978). DDD plus DDT residues in Virginia and Massachusetts eggs collected in similar areas in the 1970s (Wiemeyer et al. 1988) were similar to those found in 1986–87. The DDD and DDT residues appear insignificant with regard to potential effects on shell thickness or reproduction.

The median concentration of dieldrin did not differ between eggs collected in Virginia and Massachusetts ($Z = 1.11$, $P = 0.27$). Dieldrin was seldom detected in Virginia eggs collected from similar areas in 1976–77, whereas eggs from the Westport River, Massachusetts, collected in 1972–73 contained a mean of 0.14 ppm. The median dieldrin values in the present study are similar to mean values reported to have no significant impact on Osprey productivity (Wiemeyer et al. 1988).

PCBs were detected in all eggs from all locations and collection periods. Significantly lower PCB residues were found in eggs collected at Martin Refuge in 1986 than in 1973 ($Z = 2.606$, $P = 0.01$), suggesting a decline in the loading of PCBs. Overall, median concentrations of PCBs were significantly different among locations sampled in 1986–87 ($\chi^2 = 8.63$, $df = 2$, $P = 0.01$). Multiple comparisons did not reveal statistically significant differences between location pairs, although eggs from Martin Refuge may have contained lower residues than eggs from Virginia ($P = 0.06$) or Massachusetts ($P = 0.11$). The median PCB residue concentration for eggs from Virginia was the highest among all locations and collection periods reported in this study. Although this value is within the range of reported values for Osprey eggs collected from similar areas of Virginia in 1976–77, eggs from these areas contained mean concentrations of 5.0 to 9.2 ppm. Eggs collected from Westport River, Massachusetts, in 1972–73 contained a geometric mean of 8.3 ppm PCBs (range 2.2–23.0 ppm). PCB concentrations of the magnitude reported here have not been associated with adverse effects on Osprey reproduction (Wiemeyer et al. 1988). However, concentrations of highly toxic coplanar dioxin-like PCB cogeners and related compounds were not measured. These compounds have been implicated in reproductive impairment of fish-eating birds in other areas (Kubiak et al. 1989).

Mercury was detected in eggs from all locations and collection periods. No significant difference in mercury concentrations between collection periods was noted for eggs from Martin Refuge ($Z = 1.67$, $P = 0.09$). Further, no significant differences were detected among locations for eggs collected in 1986–87 ($\chi^2 = 0.96$, $df = 2$, $P = 0.62$). The slightly higher mercury levels found at Martin Refuge in 1986 compared to 1973 suggest that an increase in mercury contamination may have occurred. Mercury is being increasingly used in gold mining in Brazil in the Amazon Basin, much of which pollutes the aquatic environment (Martinelli et al. 1988, Pfeiffer et al. 1989). This is an important wintering area for Ospreys that breed in the Mid-Atlantic and Northeast areas of the United States (Poole and Agler 1987). Mercury concentrations in Osprey eggs were below those associated with adverse effects on reproduction (Wiemeyer et al. 1988).

DDE and PCB residues were lower in Osprey eggs collected in 1986 than in 1973 at Martin Refuge. Further, residues of DDD, DDT, and dieldrin were not detected in 1986 leading us to assume that a significant reduction in these contaminants has occurred as well. Concentrations of DDE and PCBs also appear to have declined in eggs from Virginia and Massachusetts. Although not significant, mercury residues in Osprey eggs from Martin Refuge may be increasing and warrant future monitoring. The concentrations of contaminants found appear far too low to impact nestling survival.

Geometric mean DDE concentrations in Osprey eggs from the Atlantic Coast and Delaware Bay of New Jersey that were collected in 1985–89 (Steidl

et al. 1991) bracketed the median concentration in eggs from Martin Refuge in 1986, whereas the New Jersey eggs contained somewhat higher DDE concentrations than eggs from Massachusetts and Virginia in 1986 and 1987. Dieldrin concentrations in the New Jersey eggs were similar to those we found in Virginia and Massachusetts eggs, whereas the New Jersey eggs, especially those from Delaware Bay, contained higher PCB concentrations than the eggs we analyzed. The differences in residue concentrations in Osprey eggs among these areas are an indication of exposure of the adults on their breeding areas, for they share common wintering grounds (Henny and Van Velzen 1972, Poole and Agler 1987).

Osprey eggs from Eagle Lake, California, collected after failure to hatch in 1983–84 (Littrell 1986), contained DDE concentrations similar to those in eggs from Martin Refuge in 1986. The California eggs contained much lower PCB concentrations than our samples from Virginia and Massachusetts, possibly due to the remote location of the California site from industrial contamination.

The ratios of DDE to DDD + DDT in the recent eggs from Virginia and Massachusetts compared to that in eggs from a variety of areas in earlier years (Wiemeyer et al. 1988), and the presence of DDT in all eggs from these two states suggests that these Ospreys were recently exposed to low levels of unmetabolized DDT; however, the source is unknown.

Bald Eagle (*Haliaeetus leucocephalus*) eggs from Maryland and Virginia that were collected from 15 territories after failure to hatch in 1980–84, contained geometric means of 4.4 ppm DDE, 0.42 ppm DDD + DDT, 0.31 ppm dieldrin, 14 ppm PCBs, 0.07 ppm mercury, and low concentrations of a variety of other organochlorines (S.N. Wiemeyer unpubl.). The higher concentrations of organochlorines in these eggs reflects the higher position of Bald Eagles in the food chain than that of Ospreys. Also, Chesapeake Bay Ospreys are exposed to contaminants on their breeding grounds for only about one-half of the year due to their migration, whereas breeding pairs of Bald Eagles are resident on the Chesapeake Bay.

One Peregrine Falcon (*Falco peregrinus*) egg collected in 1984 from South Marsh Island, Maryland, just to the north of Smith Island and Martin Refuge, contained 14 ppm DDE, 0.36 ppm heptachlor epoxide, 0.75 ppm oxychlordane, and 8.2 ppm PCBs (Gilroy and Barclay 1988). These elevated concentrations are also an indication of the high position of this species in the food chain and its presumed resident status in the region.

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KLEPTOPARASITISM AND CANNIBALISM IN A COLONY OF LESSER KESTRELS (*Falco naumanni*)

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Abstract.—We describe kleptoparasitism and cannibalism for the first time in a colony of Lesser Kestrels (*Falco naumanni*). Kleptoparasitism was practiced almost exclusively by females, the larger sex, while males received most of the attacks. Kleptoparasitic Lesser Kestrels had a relatively high success (43.1%, N = 52 attempts) compared to other species in which kleptoparasitism occurs frequently. Two cases of chick cannibalism by adults were also recorded.

Cleptoparasitismo y canibalismo en una colonia de Cernícalos Primillas (*Falco naumanni*).

Extracto.—El cleptoparasitismo y el canibalismo han sido observados por vez primera en una colonia de Cernícalos Primillas (*Falco naumanni*). El cleptoparasitismo fue practicado casi exclusivamente por hembras, que son de mayor tamaño que los machos, mientras que éstos recibieron la mayoría de los ataques. El éxito de los ataques fue relativamente alto (43.1%, N = 52 intentos) en comparación con el observado en otras especies donde el cleptoparasitismo es frecuente. También registramos dos casos de canibalismo practicado contra pollos por Cernícalos Primillas adultos.

Despite the fact that kleptoparasitism has been reported in several birds of prey (for a review see Brockman and Barnard 1979), it seems to be rare among species of the genus *Falco*. The Lesser Kestrel (*Falco naumanni*) is a colonial small falcon. Although both sexes do not show significant differences for most body traits, females are up to 24% heavier than their mates (Cade 1982). Males feed their females from before to a few days after egg laying, share incubation and deliver most of the nourishment for their offspring (Donázar et al. 1992). None of the authors who have studied the species described kleptoparasitic behavior (see Glutz et al. 1971, Cramp and Simmons 1980). In this study we describe the occurrence of kleptoparasitism in a colony of Lesser Kestrels and discuss the role of the reversed size dimorphism (RSD) exhibited by the species in the directionality of the kleptoparasitic attacks. Additionally, we comment on two cases of chick cannibalism by adult Lesser Kestrels.

Study Area and Methods

The observations were carried out during 1989 and 1990 in a colony of Lesser Kestrels nesting in Mairena del Alcor (37°22′N 5°45′W), Seville, southern Spain. We counted 42 breeding pairs in 1989 and 40 in 1990. A sample of nests in two adjacent walls of a tower was selected for systematic recording of behavior (see Negro et al. 1992 for details). The portion of the colony observed consisted of 7 nests in 1989 and 6 nests in 1990 (26 focal individuals). The observations of behavioral interactions, feedings and the type of prey delivered were carried out from a distance of 70 m with a telescope (20–40×). The observations lasted from dawn to dusk, 2–3 d a week, from the beginning of the period of pair formation (February) until the independence of the fledglings (end of July). Observations amounted to 475 hr in 1989 and 567 hr in 1990. Simultaneously, one or two additional observers radiotracked seven males and six females which were breeding in the portion of the colony under observation. Radiotracking amounted to 305 hr in 1989 and 647 hr in 1990.

All the nests in the colony were visited 1–3 times during the breeding season. Adults were trapped on the nest and were banded with laminated plastic bands (wearing two characters) which allowed them to be identified by telescope. In 1989 a quarter of the adult Lesser Kestrels wore these bands and in 1990 the proportion was two-thirds of the adults in the colony. All the young in the colony were also marked with plastic bands in the two years of the study.

Results

Food Supply. The availability of food in the environment was determined indirectly using feeding of nestlings as an approximate measure. The frequency of chick feedings in the colony was 1.8 feedings/hr in 1989 and 1.9 feedings/hr in 1990. Both values are below those observed in southern France (2 feedings/hr during 5.5 hr of observation; Blondel 1964 or 3.1 feedings/hr during 22.7 hr; Hovette 1971) and in northeastern Spain (5.4 feedings/hr

during 6.7 hr; M. Pomarol pers. comm.). Our values are higher, however, than those given by Bijlsma et al. (1988) for colonies in Extremadura in southwestern Spain (1.3 feedings/hr during 26 hr) where, according to the authors, the availability of food was very high. Nonetheless, these authors collected their data at the beginning of the post-fledging period, when the rate of feeding of the young is reduced (Bustamante 1990).

The prey consumed in our area might have been smaller than prey in the other studies. Most prey were insects. The percentage of vertebrates was low (0.9% of 1113 items) compared to 6.3% vertebrates observed by Franco and Andrada (1977) in the same general area several years ago, 2.6% observed in Provence (Hovette 1971), and 5.7% observed in Extremadura (Bijlsma et al. 1988).

Kleptoparasitism and Cannibalism. At least 4 individuals from the colony, but only 1 of the 26 focal individuals acted as kleptoparasites. Kleptoparasitic attacks were directed at 14 (53.8%) of these 26 focal birds. Kleptoparasitism occurred during the chick rearing period (June–July), when the parents delivered prey directly to their young in the nest. As they perched in the entrance of the nest, the attacker flew in and tried to snatch the food. Kleptoparasitic attacks were never observed while radiotracking the birds in the hunting areas, nor during the period of mate-feeding (April–May; see Donázar et al. 1992). Of the 51 attempts at stealing food, 29 (57%) failed. Of these failed attempts, 14 (48%) were because of the aggressive response by the victim, 13 (44%) were because the adult managed to transfer the food to the chicks and two (6.9%) were because the victim appeared to have anticipated the attack and escaped without feeding the chicks (although they returned later on).

Males fed chicks more than females in the period during which kleptoparasitism occurred (61.5% vs. 38.5%, $N = 894$ feedings); they were also the victims of a disproportionate number of the kleptoparasitic attacks (82.4% vs. 17.6%, $N = 51$; $\chi^2 = 9.004$, $P = 0.002$). Females were responsible for the majority of attacks (94%). Of the others, two attacks (3.9%) were made by males and one by a bird of unknown sex (goodness of fit test assuming sex ratio of 1:1, $\chi^2 = 40.50$, $P < 0.001$). When the attacker was a female, success tended to be higher when attacking males (45.2%, $N = 41$) than when attacking females (14.2%, $N = 7$), although the difference was not significant (Fisher's exact test, $P > 0.05$).

One banded female (CK) carried out 62% of the attacks. She attacked at least nine different males and four females. Another two identified females carried out one and two of the attacks, respectively. Banded but not identified females (possibly CK) carried out 13 attacks (25.4%). Another two attacks were carried out by a male and a third by an individual of unknown sex.

The importance of kleptoparasitism for the feeding of the female CK may be greater than that observed. Her nest, although near, was in a different portion of the colony so she may have made attacks which we did not observe. This female was the most successful breeder in the colony in the two years of the study. In 1989, she successfully reared three chicks when the average number of chicks fledged per breeding pair in the colony was 1.8 ± 0.17 ($N = 42$ pairs). In 1990, she successfully reared four chicks, when the average per pair in the colony was 1.4 ± 0.88 ($N = 39$ pairs).

The parasitic activity of CK was not limited to stealing food from adults carrying prey to the nest. On one occasion the fresh carcass of a 7-day-old chick, which did not correspond to any of her young, was found in her nest. On another occasion, CK was seen trying to steal a chick 10 d old from a nest. This attempt was prevented by the parent female when CK had already managed to take the chick out of the nest entrance. CK's objective was evidently the chick as she fought violently with the resident female for its possession. In 1991, we observed one adult male stealing and eating a chick in a neighboring colony.

DISCUSSION

Our data suggest that the food supply to the young by parent Lesser Kestrels was lower in the studied colony than that encountered by other investigators several decades ago in the same area or in other regions in the Western Palearctic. Additionally, we observed a high nestling mortality (about 50%) in the two years of study due to starvation (Negro 1991). Such high mortality rates have not been observed by other investigators cited here and they seem to be uncommon among raptors of similar size (e.g., Newton 1979). Both lines of evidence, the low provisioning rate and the high nestling mortality, suggest that the period of study was a time of food shortage for the Lesser Kestrels. Kleptoparasitism and cannibalism have been said to be favored in stressful

food conditions (Brockmann and Barnard 1979, Jorde and Lingle 1988, Jones and Mañez 1990, Bortolotti et al. 1991).

Kleptoparasitism was practiced mainly by female Lesser Kestrels, the larger sex, with most attacks made on males. In other species, size is apparently a determining factor for success in kleptoparasitic attempts (Knight and Knight 1988, Tershy and Breese 1990). If the frequency of kleptoparasitic attempts is influenced by the RSD (i.e., the larger size of the females) in the Lesser Kestrel, it would also be expected that males were the subject of successful attacks more frequently than females. Our results do not show a clear tendency in this respect, although this could be due to the low frequency of attacks by females on other females. It might also be that, since females spent more time in the colony throughout the breeding cycle (Donázar et al. 1992), they would have more opportunities to carry out kleptoparasitic attempts. However, the attacks were, in the main, produced at the end of the nestling period when males and females spent a similar amount of time in the colony, and not in other periods of the breeding cycle when the females' colony attendance was higher than that of males. Kleptoparasitism was practiced by a few individuals, such as the female CK, who apparently had specialized in this behavior. The systematic kleptoparasitism by the female CK may have been highly profitable, given her high reproductive success in both years of the study. We cannot discount, however, that other factors were involved, such as a high provisioning rate of her mate.

Lesser Kestrels had a relatively high success rate in their kleptoparasitic attempts (43.1%). Other species practicing intraspecific kleptoparasitism showed lower figures: Common Tern (*Sterna hirundo*) 6.2% (Hopkins and Willey 1972), Bald Eagle (*Haliaeetus leucocephalus*) 8.1% (Fischer 1985), Black Kite (*Milvus migrans*) 3.4–16.6% (Sunyer 1988). In other raptor species where intraspecific kleptoparasitism is widespread, individuals use display behaviors to hide the prey and deceive potential pirates (Brown 1976, Fischer 1985, Sunyer 1988). Such patterns of behavior were not evident in the case of the Lesser Kestrels (only 4% of the victims apparently detected the attacker). Nevertheless, in 1990 we twice observed atypical behavior by two individuals that had been recently kleptoparasitized. These males circled over the colony before feeding the chicks, and then dived to the nest.

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HOME RANGE AND ACTIVITY OF A PAIR OF BALD EAGLES BREEDING IN NORTHERN SASKATCHEWAN

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Abstract.—A male and female adult Bald Eagle (*Haliaeetus leucocephalus*) were radiotracked for 12 d during the summer of 1982. Size of the range and territory was 7 km^2 and 4 km^2, respectively. The female spent significantly more time within 200 m of the nest than the male, from 0400–1100 H. During the same period the male spent significantly more time flying than did the female. The greater proportion of time spent flying in early morning hours by the male may be a function of lower wing loading, facilitating energetically less expensive flight in the absence of updrafts and thermals. The results suggest that 400 locations of both members of a pair at 15 min intervals evenly distributed throughout the day, which is equivalent to 100 hr of observations, are adequate to describe 90% of the home range. The radio-tagged eagles usually responded only to intruders of the same sex.

Espacio habitado, y actividades de una pareja de Águila Cabeciblanca (*Haliaeetus leucocephalus*), en el norte de Saskatchewan

Extracto.—Una pareja adulta de Águila Cabeciblanca (*Haliaeetus leucocephalus*) fue radiocontrolada por 12 días durante el verano de 1982. La extensión de área habitada y el territorio a defender fueron de 7 km^2 y 4 km^2 respectivamente. La hembra pasó significativamente más tiempo que el macho dentro de 200 m cerca del nido, entre las 0400 y las 1100 horas. Durante el mismo período el macho voló significativamente más tiempo que la hembra. La mayor proporción de tiempo gastado por el macho, en sus vuelos de las tempranas horas de la mañana, puede ser una función de las alas que son proporcionalmente más grandes en relación con el peso del cuerpo; lo que facilita energéticamente menos costosos vuelos en ausencia de termales y de vientos ascendentes.

Se observaron 400 ubicaciones consecutivas con 15 minutos de intervalo de ambos miembros de esta pareja de águilas, ello es equivalente a 100 h (igualmente distribuídas durante las horas del día) de observación con ambas águilas a la vista. Estos resultados son adecuados para describir el 90% de la extensión habitada por una pareja de *Haliaeetus leucocephalus* en su ciclo reproductivo. Estas radiocontroladas águilas generalmente respondieron sólo a intrusos del mismo sexo.

[Traducción de Eudoxio Paredes-Ruiz]

Previous studies have estimated territory size and home range of breeding Bald Eagles (*Haliaeetus leucocephalus*), but in most studies estimates were based on visual locations of unmarked eagles or linear distance between nests (e.g., Broley 1947, Hensel and Troyer 1964, Retfalvi 1965, Mattson 1974, Gerrard et al. 1980, Mahaffey 1981). Radiotelemetry permits identification of individual eagles, allows locating target eagles at will, and permits more precise definition of ranges and movements.

Understanding the relative roles of male and female Bald Eagles also has been difficult due to problems identifying unmarked individuals. Similarity in plumage has made definite and continuing identification of genders difficult. Size is the best criteria for distinguishing gender of eagles in the field, and although reasonably reliable when two eagles are together, gender assignment of solitary eagles is difficult. Radiotracking eagles of known gender allows identification and improves determination of the relative roles of male and female during the breeding cycle.

Table 1. Measurements of two mated adult Bald Eagles breeding at Besnard Lake, Saskatchewan in 1982.

MEASUREMENT	MALE	FEMALE	RATIO FEMALE/MALE
Weight (g)	3920	4540	1.15
Wing span (cm)	207	211	1.02
Wing area (cm^2)	5601	6014	1.07
Wing loading (g/cm^2)	0.70	0.75	1.07
Wing			
Chord (cm)	56.8	60.3	1.06
Flattened	59.7	61.6	1.03
Culmen length (mm)	49.4	55.0	1.11
Bill depth	33.2	35.6	1.07
Tarsus (mm)			
Largest width	14.4	17.0	1.18
Smallest width	13.3	16.5	1.24
Footpad (mm)	131.3	136.9	1.04

METHODS

A pair of Bald Eagles breeding on Besnard Lake were identified through previous study and chosen for radiotagging based on logistics and previous knowledge of habits (Gerrard et al. 1983, Gerrard and Bortolotti 1988). Eagles were captured by padded leg-hold traps placed in shallow water (0.1–0.3 m deep; Harmata 1985). Four or six capture devices were set around a Northern Pike (*Esox lucius*) or Walleye (*Stizostedion vitreum*) bait carcass staked in place. One capture site was in a shallow area with a mud and rock bottom in a wide shallow bay. Emergent vegetation surrounded the capture site to prevent the eagle from attempting to take the bait by air. Another capture site was on submerged rocks near the edge of a small rocky island which had several White Spruce (*Picea glauca*) used regularly by eagles for perching. Both capture sites were within 2 m of shore where adult eagles had caught fish previously.

Each capture adult was weighed and measured; a 54 gram radiotransmitter was attached to the two central tail feathers on each eagle. Wing area was measured after tracing the outline of the right wing onto a sheet. Wing outline was later transferred to graph paper with 1 mm squares. Area was determined by counting the number of inclusive and partially inclusive squares. Wing loading is the bird's weight divided by area of the two wings (Brown and Amadon 1968) and was here expressed as grams/cm^2.

Eagles were located using receivers and hand held yagi antennae, and observed with binoculars and spotting scope. Observations were nearly continuous during daylight hours during the first 2 d. After a one day hiatus, we located both eagles at 15 min intervals from 0415–2200 H for the next 9 d. At each sampling interval we determined the location and activity of both eagles and scanned with 10× binoculars and 20–45× spotting scope to locate other eagles. Most monitoring was from an elevated rock located 1.3 km southeast of the nest. This point permitted good visibility of many of the eagles' perch sites as well as the nest. During midday, when eagles were often soaring, a mobile tracker moved throughout the eagles' range to triangulate eagles when out of visible range. Visual contact with the radio-tagged eagles was made to verify the accuracy of the telemetry locations whenever possible. Range was determined using the minimum convex polygon method (Mohr 1947, Jennrich and Turner 1969). Territory was defined as the part of the range that was defended (i.e., from which other adult eagles were excluded, Pettingill 1970). Defended area was that enclosed by locations where we saw chase flights with one or other of the territorial pair chasing other eagles away. Activity and spatial relationships were calculated by dividing the number of 15 min observation records during which the eagle was flying and more than 200 m from the nest, respectively, by total records engaged in that activity for that hourly period. Total records per period was approximately 20 in each case (range 15–22).

RESULTS

A target pair of mated adult Bald Eagles breeding on Besnard Lake was captured in July 1982. The male was captured on 17 July at the Shallow Bay site and the female on 19 July at the Rocky Island site. Both eagles were caught the same day as respective capture sites were set.

Mensural data showed considerable difference in size between the two eagles. Greatest differences were in weight, culmen length, bill depth, and tarsal width (Table 1). Measurements of the larger eagle were well within those of known females and those of the smaller eagle were well within those of known males (Bortolotti 1984).

Radiotracking of the male began after release and continued through 0900 H 28 July 1982. Male and female eagles were monitored for 126 and 105 hr over 12 and 10 d, respectively. During this time, their nestlings were between 48 and 59 d old. Both eaglets fledged normally in early August 1982.

Range and Territory. Visual locations of eagles were obtained for 48% of 964 telemetry locations. Location of the eagle monitored were equivocal as to whether it was < or >200 m from the nest for 236 of 964 telemetry locations. Range for both eagles was 7 km^2, with no appreciable differences between the range of the male and that of the female (Fig. 1). Size of range in relation to cumulative number of observations is shown in Figure 2. There was little expansion in range size during the latter half of the observation period.

The defended area was a minimum of 4 km^2 but might have been larger, particularly as few inter-

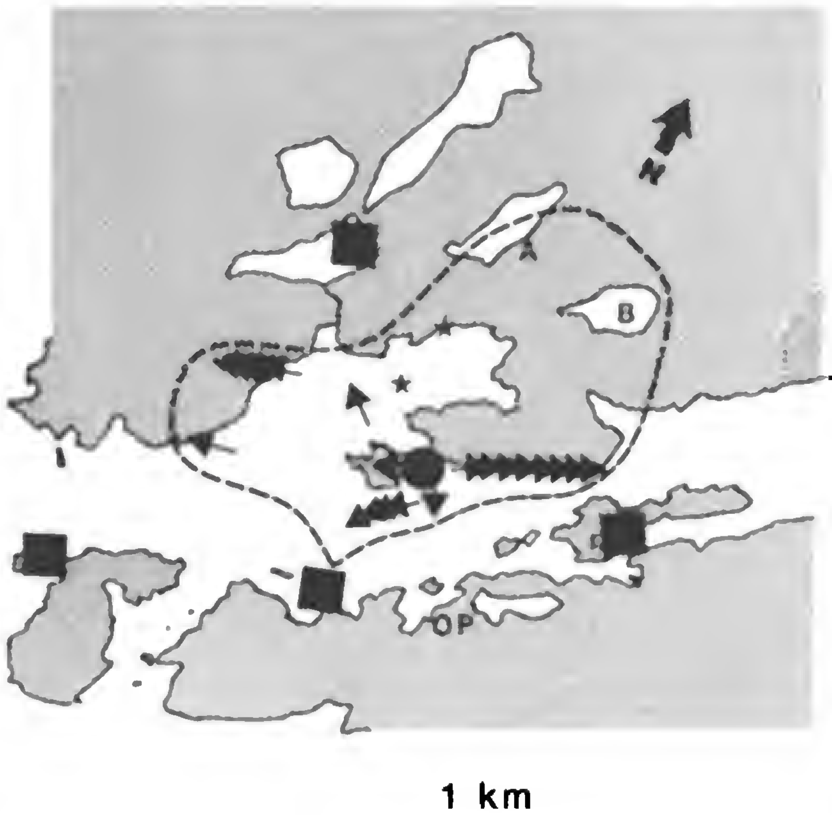

Figure 1. Range (7 km²) of a mated pair of radio-tagged Bald Eagles on Besnard Lake, Saskatchewan between 17–28 July 1982. Sightings of the male and female eagles were considered individually. The size of the range included the area encompassed by the outer extent of these flights. Symbols denote: ● nest of eagles equipped with radios, ■ nests of adjacent bald eagle pairs, → territorial defense flights by marked eagles; A, B small lakes visited by mated pair, * capture sites; OP observation hill.

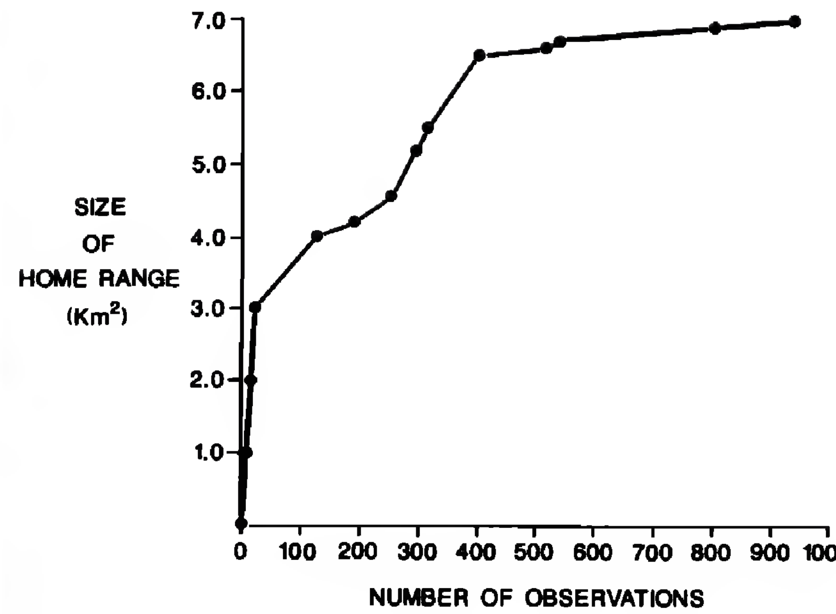

Figure 2. Size of home range of a mated pair of Bald Eagles radiotagged on Besnard Lake, Saskatchewan, in relation to cumulative number of locations.

actions were seen to the north of the nest. On three occasions when both male and female were near the nest, other adults entered the territory and perched on a small island 300 m from the nest. Size of the intruders indicated that all were females. On all three occasions, the male did not pursue the intruder but the female did. On four occasions, the male was involved in chasing and pursuing other eagles which entered the territory. Gender of intruding eagles was not determined during the latter encounters, although at least two were thought to be males.

Perching Behavior. One adult eagle was within 200 m of the nest most of the time. The female spent significantly more time within 200 m of the nest than the male from 0400–1100 H ($\chi^2 = 25.7$, $P < 0.01$; Table 2). There was no difference between male and female regarding distance from the nest from 1100–1800 H (Table 2) or from 1800–2200 H, except that the male tended to roost more than 200 m from the nest while the female roosted near the nest (Fig. 3). Both male and female used perches when near the nest. The male tended to perch on the topmost branch of the tallest spruce within 30 m of the nest (11.0% of time perched), or topmost branch of the tallest spruce on the nest island (5.2% of time perched). The female tended to perch on top of spruce trees which were slightly lower but did, on occasion, use the same perches as the male (4.7% and 0.5% of time perched, respectively). Both eagles spent a small proportion of their time away from the nest at the small lakes A and B away from Besnard Lake (4.9% for male, 6.1% for female; Fig. 1).

Activity Patterns. Activity of the eagle monitored (perched or flying) could not be determined for 228 (24%) of 964 telemetry locations. The data showed that female and male spent nearly equal time in flight, 18% and 17% respectively, but they distributed their activity differently between morning and midday. The male spent significantly more time fly-

Table 2. Spatial and temporal relationships of male and female Bald Eagles relative to their nest at Besnard Lake.

Hours	Number of Locations	
	Male	Female
0400–1100		
Within 200 m of nest	60 (31%)	93 (58%)
More than 200 m from nest	132 (69%)	67 (42%)
Total	192	160
1100–1800		
Within 200 m of nest	91 (43%)	64 (41%)
More than 200 m from nest	121 (57%)	94 (59%)
Total	212	158

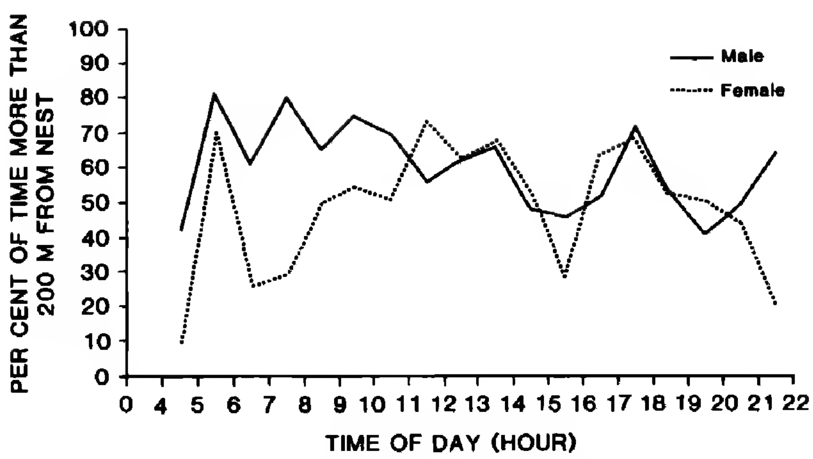

Figure 3. Location of male (——) and female (·······) Bald Eagles in relation to the location of their nest at Besnard Lake, Saskatchewan by hour of the day. Total records were approximately 20/hr.

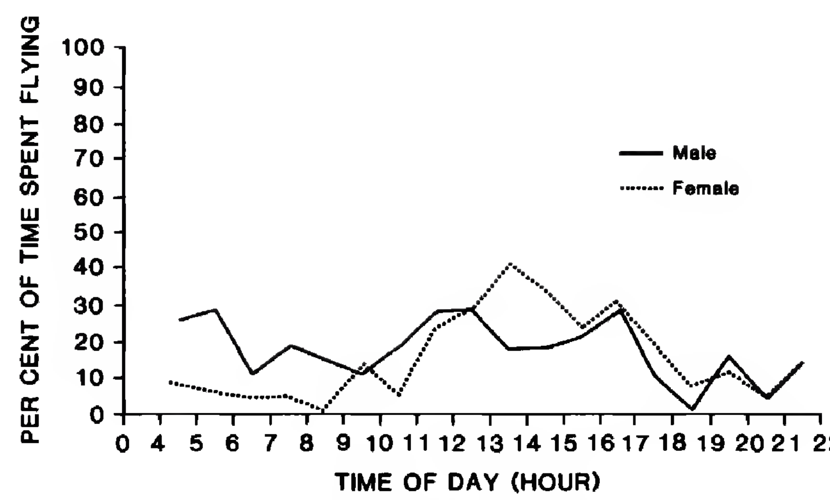

Figure 4. Percent time the radio-tagged male (——) and female (·······) Bald Eagle engaged in flight by hour of day. Total records were approximately 20/hr.

ing in early morning than did the female ($\chi^2 = 8.1$, $P < 0.01$; Table 3). There was no signficant difference in amount of time spent flying by male or female during midday, although the female tended to fly longer and/or more often (Table 3). In the evening (1800–2200 H), the flying activity of the male and female was similar (Fig. 4).

Discussion

Movements and activities of radio-tagged eagles suggested little effect of capture, handling, and monitoring on normal behavior. Upon release, the male immediately flew to perch on a tall tree on the nest island. Within 2.5 hr of release, the male had chased both an intruding immature and an intruding adult Bald Eagle and then caught a fish which it brought back to the nest. Capture and handling may have affected the female briefly, however. When released at 0820 H she did not return to the nest immediately, but flew to a perch near the small lake (B; Fig. 1) over 2 km from the nest and remained there until 1125 H. This may not have been normal behavior. Subsequent monitoring indicated that she was more often within 200 m of the nest during the morning hours. However, within 4 hr both radio-tagged eagles were using their usual perches near the nest and both the young fledged normally. Research activities apparently had no effect on habitat use or productivity.

Table 3. Relative activity of male and female Bald Eagles in early morning and during midday at Besnard Lake.

	Number of Locations	
Hours	Male	Female
0400–1100		
Flying	29 (15%)	9 (6%)
Perched	164 (85%)	152 (94%)
Total	193	161
1100–1800		
Flying	46 (21%)	46 (28%)
Perched	172 (79%)	118 (72%)
Total	218	164

Mensural data illustrated the normal size dimorphism in a mated pair of Bald Eagles. Proportionally, weight was greater for the female than wingspan and wing area, resulting in a higher wing loading. Wing loading values suggest active flight may be more energetically expensive in calm air for females than for males. Indeed, the male spent more time flying early in the day when the thermals were weaker (or non-existent). Both male and female spent considerable time flying during mid-day when thermals were strongest. Results were similar to Bald Eagle activity patterns on wintering grounds, where males tended to be active earlier and over a greater part of the day than females (Harmata 1984).

Consistent with the observation that the female was less active in the morning, she also spent more time within 200 m of the nest between 0400–1100 H. Although some bias may exist due to the proportion of locations where we did not unequivocally establish whether an eagle was more or less than 200 m from the nest or flying versus perched, we have no reason to suspect this would have differentially affected the data for males versus females. Indeed, our visual confirmation of 48% of all locations provided a reasonable corroboration of the reliability of the data. Additionally, signal characteristics differed noticeably between flying and perched eagles. Therefore, assessment of activity for eagles

out of visual range could be determined relative to signal type and receiving antenna position during strongest signal (horizontal = flying, vertical = perched).

Responses of radio-tagged eagles to intruders indicated gender-specific defense of territory. The female clearly reacted to other females but ignored eagles we thought to be males. The opposite appeared to be true for the male. Gender specific defense of territory has been noted in Golden Eagles (*Aquila chrysaetos*) and would facilitate rapid replacement of lost mates (Harmata 1982).

Home ranges of Bald Eagles vary from an estimated 10–15 km^2 for other adult eagles on Besnard Lake (Gerrard et al. 1980) to about 30 km^2 used by a pair of eagles on the San Juan Islands in Washington (Retfalvi 1965) to a mean range of 47.5 km^2 in the Greater Yellowstone Ecosystem (Harmata and Oakleaf 1991). Home ranges in the Greater Yellowstone Ecosystem were annual ranges, and this may explain the relatively large differences in relation to other estimates made during the breeding season. Size of the defended area (about 4 km^2) did not differ appreciably from an estimated 6 km^2 for a pair farther southwest on Besnard Lake, but did differ from estimates of 1.5–2.0 km^2 in Florida and Michigan (Broley 1947, Mattson 1974).

Four other pairs of eagles nested successfully in close proximity to the monitored pair (Fig. 1). These four nests were previously recorded in this region of the lake and may have induced the slightly smaller territory size relative to estimates from elsewhere on the lake in 1978 (Gerrard et al. 1980). Our findings that perches may be preferentially used by one eagle of a pair is similar to that of Retfalvi (1965) and illustrate the importance of adequately describing Bald Eagle ranges for management purposes.

Precise size of the home range of Bald Eagles may depend on available food supply and proximity of neighboring eagles. Range utilized may also vary with season, time of the breeding cycle and nesting habitat (river, lake or marine). Range size also is a function of monitoring time. Figure 2 shows little increase in size of the range after 400 observation points were accrued, suggesting that by this point we were close to determining the maximum extent of the home range.

Several recovery and management plans for the Bald Eagle in the United States suggest the development of site- or pair-specific management plans for each nesting pair before "delisting" from endangered status should occur (e.g., Pacific Bald Eagle Recovery Plan, USFWS 1986, and Montana Bald Eagle Management Plan, MBEWG 1986). The utility of site plans for effective management has been slow because the management strategy was based on an inadequate description of range and habitat use. Data deficiencies were mostly a consequence of insufficient monitoring effort, spawned by a lack of guidelines.

In this study, 400 consecutive 15 min telemetry locations determined 93% of the range of a pair of Bald Eagles. Doubling the effort added only 7% to range size (Fig. 1). Therefore, a minimum of 400 telemetry locations, accrued consecutively at 15 min intervals over daylight hours, or 100 hr of observation with both eagles in view, distributed evenly throughout daylight hours may be used as a guideline for observational effort. This effort should delineate over 90% of a range of breeding Bald Eagles and provide adequate data for site- or pair-specific management purposes, at least on lakes.

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SEASONAL AND SEXUAL VARIATION IN THE DIET OF THE COMMON BUZZARD IN NORTHEASTERN SPAIN

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Abstract.—We examined the diet of Common Buzzards (*Buteo buteo*) from a Mediterranean area (Catalonia, NE Spain), by analyzing prey remains and pellets found in the nest, and stomach contents. The diet was seasonal. Relatively large items, such as young rabbits and Ocellated Lizards (*Lacerta lepida*), predominated in the breeding season, orthopterans and mantodeans in autumn and insects, rodents and soricidans in winter. Males presented an empty stomach more often than females, but only small differences were found in the diet of males and females.

Resumen.—Se analiza la variación estacional en la dieta del ratonero común (*Buteo buteo*) en una zona mediterránea (Cataluña, NE España) a base de restos de presas y egagrópilas encontrados en los nidos y al análisis de contenidos estomacales. La dieta varió estacionalmente. Durante el período reproductivo, el ratonero consumió presas relativamente grandes, tales como gazapos y lagartos, mientras que en otoño consumió preferentemente ortópteros y mántidos. En invierno los insectos, roedores y musarañas constituyeron la base de la dieta. Los machos presentaron el estómago vacío con mayor frecuencia que las hembras pero sólo se detectaron pequeñas diferencias en la dieta de ambos sexos.

The Common Buzzard (*Buteo buteo*) feeds on a wide range of prey, mainly rodents, but also on other vertebrates and invertebrates of appropriate size (Cramp and Simmons 1980). Its diet has been studied in most parts of its geographical range, and it reflects underlying differences in prey availability (Bustamante 1985). However, seasonal variation has received much less attention, probably because of difficulty in studying the diet outside the breeding season. In this paper we investigate the seasonal variation of the diet of the Common Buzzard in a Mediterranean area, where the species is present throughout the year.

Study Area and Methods

Diet outside the breeding season was studied by analyzing the stomach contents of 69 Common Buzzards confiscated from hunters in the Mediterranean area of Catalonia (NE Spain) between October and February of 1982-87 The sex of 39 individuals was identified. Diet during the breeding season was studied in La Segarra county of Catalonia by collecting prey remains and pellets from 20 nests, during and after reproduction in 1985-89. Pellets were especially useful to identify small prey, which are rarely found as items in the nest (Mañosa 1991, Real 1991). The importance of each prey was expressed as the percentage of appearance of that prey among all prey items in nests, pellets or stomachs.

Results and Discussion

Diet During the Breeding Season (Spring-Summer). European Rabbit (*Oryctolagus cuniculus*) was the most frequent prey species (Appendix 1). This has been found in other Mediterranean areas (Veiga 1982, Real 1987) but is unlike the deciduous forest region of Northern Spain where invertebrates form the bulk of the diet (Bustamante 1985). The Common Buzzard captured mainly young rabbits, very abundant in spring and summer (Soriguer 1981). The mean tarsus length of the rabbits taken was 37.5 mm (SD = 5.7, range = 26-64, N = 122), which corresponds to a mean weight of less than 550 g (Mañosa 1991). The second most consumed prey were reptiles, especially Ocellated Lizard (*Lacerta lepida*), also very common in spring and summer (Castilla 1989). Several species of birds formed an important percentage of the diet. Invertebrates, amphibians, rodents and shrews were taken only occasionally (Table 1).

Diet Outside the Breeding Season. Only 45 (65%) of the 69 stomachs analyzed contained at least one prey. A total of 240 prey items were found (Appendix 1). Insects were the most frequent prey both in autumn and winter (Table 1). Rabbits were

Table 1. Diet of Common Buzzard in Catalonia (NE Spain) expressed in percentages. Autumn includes October–November, winter December–February and spring and summer the breeding season.

	Spring and Summer				
	Remains	Pellets	Autumn	Winter	Autumn and Winter
Mammals	69.90	49.75	7.28	38.2	18.74
Shrews	0.33	0.00	0.00	15.73	5.83
Rabbits	66.55	21.89	0.66	2.25	1.25
Voles	0.00	6.47	3.31	6.74	4.58
Mice	1.34	5.47	1.32	10.11	4.58
Other mammals	1.67	15.92	1.99	3.37	2.50
Birds	16.50	12.44	0.00	3.37	1.25
Reptiles	13.88	35.82	3.31	3.37	3.33
Amphibians	0.17	0.00	0.66	7.87	3.33
Insects	0.00	1.99	87.42	43.82	71.26
Mantodeans	0.00	0.00	31.79	17.98	26.67
Orthopterans	0.00	1.49	54.97	19.10	41.67
Coleopterans	0.00	0.50	0.66	6.74	2.92
Other invertebrates	0.00	0.00	1.32	3.37	2.08
Total	598	201	152	88	240

taken only occasionally, and rodents and shrews were the most common mammalian prey. Because of the low temperatures, reptiles are not available during the autumn and winter periods (Castilla 1989), and their presence in the diet was restricted. In winter, most insect populations decrease, and small mammals (rodents and shrews) increase in their importance in the diet. Then they are especially abundant in open fields, where they lack cover as they feed. Amphibians increased their presence in the winter diet, when they concentrate around their breeding pools (Valverde 1967).

Seasonal and Sexual Comparison. Compared with pellet analysis, collections of prey remains in nests underestimates small preys (invertebrates, small mammals and reptiles). On grouping prey into invertebrates, poikilotherm vertebrates, birds, rabbits, and small mammals, differences were significant ($\chi^2 = 199.038$, df $= 4$, $P < 0.01$; Table 1). We analyzed seasonal variation by comparing pellet data with stomach contents, eliminating by this way the bias associated with prey remain collections. On grouping prey into invertebrates, amphibians, reptiles, birds, rabbits and small mammals, we found differences between breeding-season, autumn and winter diets ($\chi^2 = 341.436$, df $= 10$, $P < 0.01$; Table 1). Buzzards consumed bigger prey during the breeding season than outside it, but it is possible that adults carried only large prey to the nests and consumed small prey themselves, as was observed in other raptors (Veiga 1982, Donázar 1988). This possibility should be taken into account when interpreting our results. The sex ratio of buzzards killed did not differ significantly from unity (20 males and 19 females; $\chi^2 = 0.026$, $P > 0.05$) with no variation between autumn and winter ($\chi^2 = 0.779$, $P > 0.05$). Data from

Table 2. Frequency of full compared to empty stomachs according to sex of Common Buzzards.

	Males	Females	Total
Full	9	17	26
Empty	10	3	13
Total	19	20	39

Table 3. Number of Common Buzzard stomachs in which different prey were found in relation to sex.

	Males ($N = 9$)	Females ($N = 17$)
Invertebrates	5	8
Amphibians	3	0
Reptiles	1	2
Birds	1	1
Rabbits	0	2
Small mammals	8	10

both seasons could therefore be pooled to analyze differences in diet between the sexes. Empty stomachs were found more often in males than females ($\chi^2 = 6.278$, $P < 0.025$; Table 2). Although sample sizes were small, we found amphibians more often in stomachs of males than females (Fisher exact test $P = 0.03$) and Rabbits were taken only by females (Table 3). These differences may be related to the sexual dimorphism of the species (male weight = 828 g, female weight = 1052 g; Cramp and Simmons 1980) and can be explained either by prey selection or by habitat partitioning, as shown in Hen Harriers (*Circus cyaneus*; Newton 1979, Marquiss 1980), European Sparrowhawks (*Accipiter nisus*; Marquiss and Newton 1982, Newton 1986), or American Kestrels (*Falco sparverius*; Smallwood 1987, 1988).

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Appendix 1. Prey items of the Common Buzzard during the breeding and non-breeding season in Catalonia (NE Spain). Species with less than five representatives are grouped in the "other" category.

	Breeding Season				Fall and Winter	
	Remains		Pellets			
	N	%	*N*	%	*N*	%
Mammals	416	69.60	100	49.75	445	18.75
Crocidura russula	2	0.33			11	4.58
Oryctolagus cuniculus	398	66.55	44	21.89	3	1.25
Sciurus vulgaris	4	0.67	15	7.46		
Microtus duodecimcostatus			13	6.47	11	4.58
Apodemus sylvaticus	6	1.00	11	5.47	7	2.92
Other[a] mammals	6	1.00	2	1.99	7	2.92
Unidentified small mammals			15	7.46	6	2.50
Birds	96	16.05	25	12.44	3	1.25
Alectoris rufa	30	5.02			1	0.42
Columba palumbus	15	2.51				
Garrulus glandarius	11	1.84				
Unidentified Passeriformes	12	2.01	17	8.46		
Other[a] birds	12	2.01			2	0.83
Unidentified birds	16	2.67	8	3.98		
Reptiles	83	13.88	72	35.82	8	3.33
Psammodromus algirus	7	1.17	24	11.94		
Lacerta lepida	44	7.36	25	12.44		
Ophidians	31	5.18	8	3.98	1	0.42
Other[a] reptiles	1	0.17			7	2.92
Unidentified reptiles			15	7.46		
Amphibians	1	0.17			8	3.33
Bufo sp.					5	2.08
Other[a] amphibians	1	0.17			3	1.25
Arthropods			4	1.99	175	72.92
Mantis religiosa					64	26.67
Grillotalpa grillotalpa					13	5.42
Unidentified Acrididae					5	2.08
Other orthopterans			3	1.49	6	2.50
Coleopterans			1	0.50	7	2.92
Other[a] arthropods					4	1.67
Anelids					1	0.42
Oligochets					1	0.42
Total prey	598		201		240	

[a] Other prey items include: Mammals: *Suncus etruscus, Eliomys quercinus, Rattus rattus, Mus spretus, Mus* sp., Unidentified Muridae, *Mustela nivalis*. Birds: *Columba oenas, Otus scops, Athene noctua*, Alaudidae, *Saxicola torquata, Turdus merula, Turdus viscivorus, Oriolus oriolus, Sturnus vulgaris, Fringilla coelebs, Emberiza cirlus, Miliaria calandra*, Nestling Passeriforme. Ophidians: *Malpolon monspessulanus, Elaphe scalaris*, Unidentified Ophidians. Reptiles: *Podarcis hispanica, Blanus cinereus, Natrix natrix, Natrix* sp., *Anguis fragilis, Vipera latastii*. Amphibians: *Bufo calamita, Hyla meridionalis, Rana perezi*. Coleopterans: Tenebrionidae, Carabidae, *Timarcha tenebricosa, Cetonia aurata, Geotrupes stercorarius*, Unidentified Coleopterans. Orthopterans: *Gryllus campestris, Oedipoda* sp., *Anacridium* sp., Unidentified Orthopterans. Arthropods: *Camponotus cruentatus*, Lepidoptera Larvae, *Disdera* sp., Unidentified Isopoda.

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DIET CHANGES IN BREEDING TAWNY OWLS (*Strix aluco*)

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ABSTRACT.—I examined the contents of Tawny Owl (*Strix aluco sylvatica*) pellets, between April 1977 and February 1978, in mixed woodland and gardens in northeast Suffolk, England. Six mammal, 14 bird and 5 invertebrate species were recorded in a sample of 105 pellets. Overall, the Wood Mouse (*Apodemus sylvaticus*) was the most frequently taken mammal prey and the House Sparrow (*Passer domesticus*) was the most frequently identified bird prey. Two types of seasonal diet change were found; first, a shift from mammal prey in winter to bird prey in the breeding season, and second, a shift from small prey in the winter to medium-sized (>30 g) prey in the breeding season. Contrary to some findings elsewhere in England, birds, rather than mammals, contributed significantly to Tawny Owl diet during the breeding season.

Cambios en la dieta de búhos de la especie *Strix aluco* durante el período de reproducción

EXTRACTO.—He examinado el contenido de egagrópilas del búho de la especie *Strix aluco sylvatica,* entre abril de 1977 y febrero de 1978, en florestas y huertos del noreste de Suffolk, Inglaterra. Seis mamíferos, catorce aves y cinco especies invertebradas fueron registrados en una muestra de 105 egagrópilas. En el total, entre los mamíferos, el roedor *Apodemus sylvaticus* fue el que con más frecuencia fue presa de estos búhos; y entre las aves, la presa identificada con más frecuencia fue el gorrión *Passer domesticus.* Dos tipos de cambio en la dieta estacional fueron observados: primero, un cambio de clase de presa: de mamíferos en invierno a la de aves en la estación reproductora; y segundo, un cambio en el tamaño de las presas: de pequeñas en el invierno a medianas (>30 g) en la estación reproductora. En contraste con hallazgos realizados en otras partes de Inglaterra, las aves, en vez de los mamíferos, contribuyeron significativamente a la dieta del *Strix aluco sylvatica* durante las estación reproductora.

[Traducción de Eudoxio Paredes-Ruiz]

The diet of many owl species is influenced by habitat and season (e.g., Marti 1974, Yalden 1985, Mikkola 1983). Among sedentary "generalist" species, Tawny Owls (*Strix aluco sylvatica*) inhabiting deciduous woodland in England preyed on Bank Voles (*Clethrionomys glareolus*) and Wood Mice (*Apodemus sylvaticus*) in winter, but switched to Moles (*Talpidae*), young Rabbits (*Oryctolagus cuniculus*), Cockchafers (*Melolontha melolontha*) and earthworms (*Lumbricina*) in summer (Southern 1954, 1969). In urban or other open habitats, birds may form important components of Tawny Owl diet (e.g., Harrison 1960, Beven 1965, Yalden and Jones 1971, Glue 1972), but these have generally been aggregated in analyses so that the seasonal importance of different species or size classes cannot be investigated.

Few data exist with regard to Tawny Owl diet in discontinuous woodland habitats, where prey species and hunting techniques may differ from that of owls inhabiting larger forest tracts (Nilsson 1978). In this paper, I report on seasonal variation in the diet of Tawny Owls from a site in south-eastern England in relation to breeding and possible changes in prey selection or availability. Because Tawny Owls disgorge pellets before roosting (Guérin 1932), pellets are scattered throughout territories, making them difficult to find. However, in this study sufficient numbers of pellets were found by intensive searching and knowledge of roost sites of individual owls.

STUDY AREA AND METHODS

This study was carried out between April 1977 and February 1978 at Herringfleet, north-east Suffolk, in a 0.06 km^2 woodland dominated by Scots Pine (*Pinus sylvestris*), with mixed woods of birch (*Betula pendula*), oak (*Quercus robur*), rowan (*Sorbus aucuparia*), maple (*Acer platanoides*) and ash (*Fraxinus excelsior*), interspersed with large gardens. Marshes used for grazing and reedbeds (*Phragmites australis*) occur along a river to the west and

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Table 1. Total numbers and percentage contribution by weight of prey species recovered in Tawny Owl pellets, during and outside the breeding season (April–August; non-breeding season September–February).

Prey Species	Breeding Season No.	Breeding Season Weight (g)	Breeding Season % Weight	Winter Season No.	Winter Season Weight (g)	Winter Season % Weight
Common Shrew *Sorex araneus*	0	0	0	1	8	0.3
Wood Mouse *Apodemus sylvaticus*	4	72	4.4	34	612	20.7
Field Vole *Microtus agrestis*	0	0	0	14	294	10.0
Bank Vole *Clethrionomys glareolus*	1	16	1.0	29	464	15.7
Rabbit *Oryctolagus cuniculus*	1	100	6.1	0	0	0
Norway Rat *Rattus norvegicus*	3	180	10.9	4	240	8.1
Kestrel *Falco tinnunculus*	1	220	13.3	0	0	0
Wren *Troglodytes troglodytes*	0	0	0	1	8	0.3
Dunnock/Robin *Prunella modularis/Erithacus rubecula*	1	20	1.2	1	20	0.7
Blackbird/Song Thrush *Turdus merula/T. philomelos*	7	599	36.3	3	257	8.7
Redwing/Starling *Turdus iliacus/Sturnus vulgaris*	0	0	0	5	368	12.5
Coal Tit/Blue Tit *Parus ater/P. caeruleus*	0	0	0	4	48	1.6
Jay *Garrulus glandarius*	1	161	9.8	0	0	0
Starling *Sturnus vulgaris*	2	164	9.9	0	0	0
House Sparrow *Passer domesticus*	0	0	0	12	294	10.0
Chaffinch *Fringilla coelobs*	0	0	0	2	49	1.7
Greenfinch *Carduelis chloris*	0	0	0	2	52	1.8
Small bird (unidentified)	5	100	6.1	10	200	6.8
Dor beetle *Geotrupes stercocarius*	0	0	0	30	30	1.0
Dung Beetle *Typhaeus typhoeus*	13	13	0.8	6	6	0.2
Cockchafer *Melolontha melolontha*	4	4	0.2	0	0	0
Beetles Carabidae	0	0	0	4	0.4	0.01
Earthworms Lumbricidae	1	0	0	34	0	0
Total	43[a]	1649		162[a]	2950	

[a] Excluding earthworms.

farmland to the east. Exotic shrubs such as rhododenron (*Rhododendron* spp.) and laurel (*Prunus laurocerasus*) provide roosts for small birds during winter.

I collected pellets at weekly intervals at roosts in 2–3 ha of mature Scots Pine in two large wooded gardens. Of the 105 pellets, 77% were collected during the first 5 mo, the remaining 23% were collected between September and February. One pair of Tawny Owls nested in a nestbox, approximately 300 m from the roost sites used for pellet collection. However, few pellets were found beneath the nestbox. The principal source of pellets was from this pair of owls but due to territorial infringements some pellets might have been from other individuals (territories in discontinuous woodland in Wytham averaged 22 ha; Hirons 1985). I collected up to 16 pellets per week from October–February (21% of pellets cast by owls, assuming 1.27 pellets/day are produced in winter; Lowe 1980), but between April and September relatively few pellets (1–6 per week) were found (6% of pellets cast, assuming 1.03 pellets/day are produced in summer) for the reasons described by Southern and Lowe (1968).

Mammal remains were identified to species by dental and cranial features (Yalden 1977), while birds were identified by comparing skulls or bills with reference skeletons collected locally. Other remains used to identify birds were feet, pelvises, gizzard size and feathers in the pellet matrix. The number of individuals represented was determined by counts of skulls, jaws or pelvises for mammals, and skulls, mandibles and long bones for birds as suggested by experiments with Tawny and other owl species (Short and Drew 1962, Raczyński and Ruprecht 1974).

Coleoptera were identified by elytra striations and chitinous remains. Earthworms were identified by chaetae and I estimated earthworm numbers by the proportion of fibrous material and sand in pellets (Southern 1954). Estimates of earthworms were excluded from table totals because they were not comparable with counts of other prey. Average weights of bird species were calculated by the length of humeri recovered in pellets using the regression equation; log weight = (2.706 × log humerus length) − 2.062 (Yalden 1977) or by using average weights in Hickling (1983, Appendix 12). I used data in Yalden (1977, 1985) for weights of small mammals and Coleoptera.

Results and Discussion

I recorded 6 mammal, 14 bird and 5 invertebrate species in the 105 pellets examined (Table 1). Of a total of 204 prey items recovered from pellets (ex-

cluding earthworms), 45% by number were mammals. Wood Mice predominated (19%), followed by Bank Voles (15%) and Field Voles (7%). Birds comprised 28% of total prey; birds smaller than 30 g estimated body weight contributed 19%. Of the species identified, House Sparrows (6%) and thrushes (*Turdus* spp. 5%) were most important. Numerically, Coleoptera represented 30% of total diet. By weight, mammals formed 43% and birds 56%, respectively. European Blackbirds and Song Thrushes were most important by weight (19%), followed by Wood Mice (15%), Bank Voles (10%) and Norway Rats (9%). The contribution of Coleoptera by weight was negligible.

Significantly more birds than mammals were taken between April–August than between September–February ($G = 8.08, P < 0.005$), suggesting a switch from small rodents to birds during the breeding period. Also, significantly more medium-sized than small vertebrate prey were taken by owls during the breeding season than in autumn and winter when the converse was true ($G = 24.29, P < 0.001$; Table 2). Similar results were found when bird prey were considered separately ($G = 8.57, P < 0.005$), although the total biomass intake of small and medium-sized birds was similar between the breeding and non-breeding season (Table 2). The weight of vertebrate prey was significantly higher in the breeding than the non-breeding season (breeding season $\bar{x} = 62.8$ g, SE = 9.7, $N = 26$; non-breeding $\bar{x} = 23.9$ g, SE = 1.5, $N = 122$; Mann Whitney U test, $Z = 4.473, P < 0.001$), but no difference was found when invertebrates were included.

During the breeding season, thrushes, European Starlings, Jay, and Eurasian Kestrel together contributed 69% of the diet by weight. Wood Mice and Bank Voles comprised only 5%. In winter, Wood Mice, Bank Voles, Field Voles and Common Shrews accounted for 47% of the diet by weight. Small birds (e.g., House Sparrows) comprised 23% of the winter diet by weight (Tables 1 and 2). Earthworms were taken mostly in the non-breeding season, particularly in October and December, probably due to the wet conditions in these months resulting in increased availability of earthworms. The importance of earthworms was probably greatly underestimated since I did not weigh the granular content of pellets as recommended by Yalden (1985). Two species of dung beetles (*Geotrupes stercocarius* and *Typhaeus typhoeus*) were also taken in large numbers. *Geotrupes* occurred in pellets most frequently in autumn and winter, showing that Tawny Owls foraged over marshes where there were cattle. *Typhaeus* was most commonly taken in the summer (Table 1). Cockchafer beetles were found in pellets from June and July, the period of emergence for this species.

Table 2. The contribution of different-sized prey in Tawny Owl diet during and outside the breeding season (percentage figures refer to weight of prey items in grams).

	Breeding Season (24 Pellets)		Winter Season (81 Pellets)	
	No.	% Weight (g)	No.	% Weight (g)
Small mammals	5	5.3	78	46.7
Medium-sized mammals	4	17.0	4	8.1
Small birds	6	7.3	32	22.7
Medium-sized birds	11	69.4	8	21.2
Invertebrates[a]	18	1.0	44	1.2
Total number	43		166	
Total weight		1649		2950

[a] Excluding earthworms.

A shift from small to larger (mammal) prey in Tawny Owl diet during the breeding season was also found in Derbyshire, England, but in contrast to my study bird prey was most important in the 'winter' season (Yalden 1985, Table 2). Increased weight of prey taken by Tawny Owls during the breeding season was suggested by Nilsson (1984) in Sweden, and by Southern (1954) in Oxfordshire, England. However, in the latter study owls apparently did not prey on abundant fledgling passerines.

The increase in medium-sized (often fledgling) bird prey in this study during the breeding season suggested that Tawny Owls might selectively take larger prey when they have chicks, as noted by Mikkola (1983, Table 26) and as documented in some Common Barn Owl (*Tyto alba*) pairs (Buckley and Goldsmith 1975). Southern (1969) also recorded diet changes in Wytham owls when their young were half-grown and no longer brooded. Tawny Owls are sexually dimorphic, and the larger size of females (26% heavier than males; Hardy et al. 1981) might allow them to select larger prey than the male (for other owl species see Earhart and Johnson 1970, Mikkola 1983), especially when they have limited hunting time due to demands from their chicks. Also, individual Tawny Owls can specialize on particular prey types, so perhaps the female owl in this study selectively took large bird prey at this time. Conversely, more small birds were found in winter pel-

lets probably as a result of owls feeding on communally roosting birds as occurs in Long-eared Owls (*Asio otus;* Glue and Hammond 1974).

Prey availability for Tawny Owls is determined by ground cover (Southern and Lowe 1968) which may account for seasonal change in the diet of Tawny Owls at Herringfleet. Dense vegetation cover (especially Bracken *Pteridium aquilinum*) in summer could prevent owls from locating small mammal prey. Conversely, dieback of vegetation in autumn may mean that small rodents are more vulnerable to owl predation. Rodents might make more noise moving through leaf litter on the ground in autumn and winter and thus be more easily located by foraging owls. The fact that a major prey species, the Wood Mouse, spends less time foraging outside the nest in winter on moonlit nights (Wolton 1983) also indicates that small mammals are more vulnerable to Tawny Owl predation in the winter season. Thus, changes in vegetation cover could account for the abundance of small rodents in Tawny Owl diet at Herringfleet during the winter season.

My results suggest one, or a combination of factors in the apparent diet shift; 1) small mammals were more vulnerable to owl predation outside the breeding season; 2) owls switched, opportunistically, to fledgling birds during the breeding season because they were easier to catch or 3) medium-sized birds were taken selectively by owls because they were more 'profitable' prey (with a higher nutrient intake per handling time) than rodents, during the period when owls had dependent young.

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FORAGING ECOLOGY OF BALD EAGLES ON A REGULATED RIVER

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ABSTRACT.—We studied the habitat, foraging behavior, and prey of eight pairs of Bald Eagles (*Haliaeetus leucocephalus*) nesting along northern California's Pit River where flows and reservoir elevations were regulated by five hydroelectric facilities. Prey remains ($N = 1166$) and photographic data ($N = 117$) indicated that eagles fed on a variety of fishes (88%), birds (9%), and mammals (4%), but one species, Sacramento Sucker (*Catostomus occidentalis*) dominated the diets of all pairs. Bald Eagle prey utilization at Britton Reservoir was directly related to the abundance of fish species inventoried by surface gill nets. Bald Eagles ate Sacramento Sucker and Tule Perch (*Hysterocarpus traski*) as carrion in late May, June, and July when these species became numerous on the surface of the reservoir. Eagles nesting near relatively small run-of-river reservoirs downstream of Britton Reservoir foraged in both lacustrine and riverine habitats. On the river sections, eagles selected hunting perches near pools rather than runs or riffles. In pools, live suckers were taken mainly in shallow areas where there was no surface turbulence. Inventories indicated that fish were less common in pools than in runs or riffles, suggesting that physical conditions promoting prey vulnerability were more important to eagles than those influencing prey density. However, eagles did not use a large section of river where suckers of appropriate sizes for eagles were uncommon.

Hábitos de alimentación de Águila Cabeciblanca en un río de corriente regulada

EXTRACTO.—Hemos estudiado el hábitat, la conducta en la alimentación, y las presas de ocho parejas de Aguila Cabeciblanca (*Haliaeetus leucocephalus*) que anidaban a lo largo de río Pit en California del norte. En este río el volumen del flujo del agua y la cantidad de ella en las represas estaban regulados por medio de cinco plantas hidroeléctricas. Los residuos de presas ($N = 1166$) así como datos fotográficos ($N = 117$) indicaron que las águilas se alimentaron de una variedad de peces (88%), de aves (9%), y de mamíferos (4%); pero una especie de pez perteneciente a la especie *Catostomus occidentalis* dominó la dieta de todas las parejas. La utilización de las presas de Águila Cabeciblanca en la represa Britton, estuvo directamente relacionada con la abundancia de especies de peces cogidos por redes tendidas en la superficie del agua. Hacia fines de mayo, en junio y julio, las águilas comieron carroña de peces *C. occidentalis* y *Hysterocarpus traski*, cuando estas especies se hacen numerosas en la superficie del estanque. Águilas que anidaban cerca de relativamente pequeños estanques, los que se llenan con agua de la represa Britton, se alimentaron tanto en hábitats lacustres como fluviales. En las secciones rivereñas, las águilas seleccionaron las perchas de observación para cazar prefiriendo la cercanía a albercas que a corrientes rápidas o turbulentas. En las albercas, peces vivos fueron cogidos principalmente en áreas de poca profundidad donde no había turbulencia superficial. Los conteos indicaron que los peces fueron menos numerosos en albercas que en secciones de rápidos y turbulencias; lo que sugiere que las condiciones físicas que promueven la vulnerabilidad de las posibles presas, fueron más importantes para las águilas que las condiciones que influencian la abundancia de las presas. Sin embargo, las águilas no usaron una gran sección del río donde los peces del tamaño apropiado para ellas no fueron comunes.

[Traducción de Eudoxio Paredes-Ruiz]

Foraging success of raptors depends on the composition, densities, life histories, and behaviors of prey species, and the physical and biotic elements of habitat that contribute to prey vulnerability. Raptor foraging patterns may coincide with prey abundance (Hunt et al. 1992a) or depend on the distribution

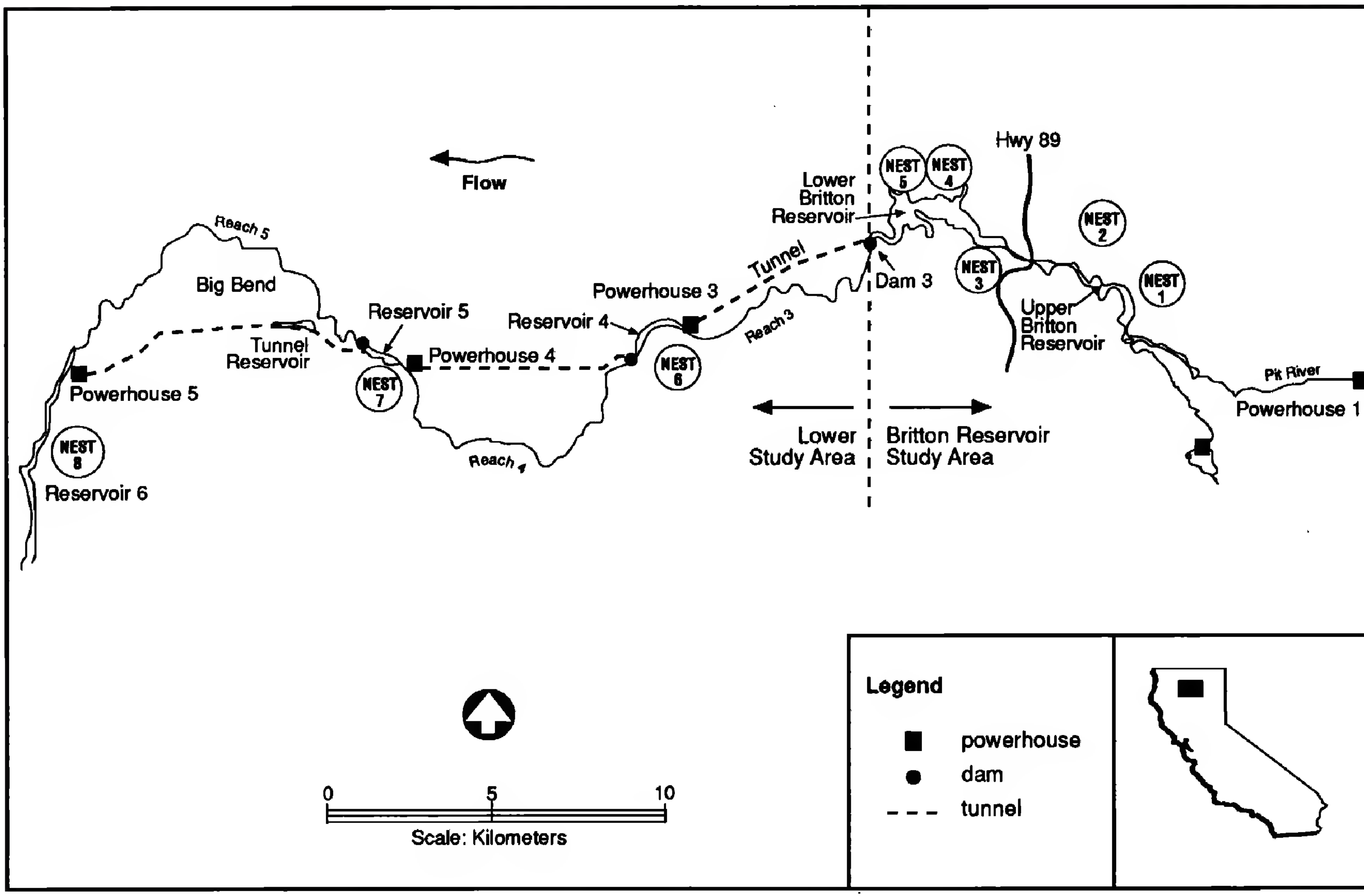

Figure 1. The Pit River study area in northern California.

of specific habitats where prey are vulnerable but not necessarily abundant (Hunt and Ward 1988). Life history, behavioral, and ecological factors affecting vulnerability may differ among prey species and habitats.

In this paper, we present the results of a two-year study on the foraging ecology of Bald Eagles (*Haliaeetus leucocephalus*) on northern California's Pit River, where flows are controlled by five hydroelectric facilities occurring along 70 river km (study area). Eight Bald Eagle nesting territories are known in the area, and in winter and spring eagle numbers are augmented by migrants.

To explore the interrelationships between eagle diet, foraging habitat selection, and factors affecting prey availability, we investigated: 1) the distribution of nesting and wintering eagles in the study area using visual surveys and telemetry, 2) diets of the eagles, 3) habitat use in both lacustrine and riverine habitats, 4) river habitat distribution, 5) distribution, relative abundance, and size classes of prey species, and 6) how each major prey fish species became vulnerable to Bald Eagles.

STUDY AREA

The Pit River originates in the Warner Mountains of northeastern California and flows through several broad, irrigated valleys to Fall River Mills where it enters a narrow, steep-sided canyon that extends for 90 km to Shasta Reservoir. Our study area included 70.3 km of this canyon, from the river section upstream from Britton Reservoir downstream to Reservoir 6 (Fig. 1). Within this zone are 24.5 km of reservoirs (Britton Reservoir and Reservoirs 4, 5, and 6) and 45.8 km of flowing, regulated river (Reaches 3, 4, and 5). Rather than producing electric power at Dams 3, 4, and 5, water is transported from them in underground conduits to powerhouses (turbines) located 10–16 river km downstream near the inflow of the next reservoir.

Because of habitat differences, we distinguish between Britton Reservoir (13 km long, 520 ha) and the mainly riverine environment downstream from it (Lower Study Area) where two relatively small run-of-river (currented) reservoirs (Reservoirs 4 and 5, 42 ha and 13 ha respectively) lie between river sections 9.6 to 15.9 km in length. In discussions of the river reaches, we sometimes differentiate between the upper (upstream) and lower (downstream) halves of each reach.

The area around Britton Reservoir is primarily Ponderosa Pine (*Pinus ponderosa*) forest (elevation ca. 860 m MSL); Sierran mixed-conifer forest is the dominant habitat type in the lower study area (elevation at Pit 6 Dam ca. 430 m MSL). Rainfall averages about 1 m/yr. Rec-

reational use peaks during May–October and includes fishing and camping throughout the study area, and boating on Britton Reservoir.

In warmer months, the level of Britton Reservoir fluctuates with power demand, resulting in a highly variable pattern of drawdown (1–2 m/wk) during weekdays and refilling during weekends. Flashboards raise the height of the dam almost 2 m and increase generating capacity; they are removed in winter when increased flows result in spillage over the dam. The reservoir is often turbid with algae, particularly in the warmer months.

The three river reaches (3, 4, and 5) are confined to narrow canyons and have coarse-textured substrates, mostly cobbles and boulders covered with algae. During spring runoff, flow rates in the reaches are about 100 m^3/sec and, rarely, up to 565 m^3/sec. In the summer, Dams 4 and 5 provide minimum flow releases into the river sections of 1.4–4.2 m^3/sec on behalf of fisheries (D. Bowers pers. comm.). During our study, no water was released from the dam at Lake Britton (Dam 3), but about 1.4 m^3/sec seeped from the dam and underground springs. Because none of the warm turbid water from Britton Reservoir was released into Reach 3 in summer, water was cooler and clearer than in reaches 4 and 5. The fish community in Reach 3 reflected these differences.

METHODS

Bald Eagle Distribution and Habitat Selection. We determined the distribution of Bald Eagles in the study area by censuses conducted from helicopters, boats, and vehicles. We made 82 helicopter censuses from a Bell Jet Ranger helicopter, flying at 95–125 km/hr downriver or along reservoir shores above the tree tops. Weather permitting, these censuses were done weekly from March 1983 to December 1984, usually in the early morning. On Britton Reservoir, we censused Bald Eagles and waterfowl on 36 surveys (approximately 2/mo) from a boat moving slowly along the shore. At Reservoir 4, we censused Bald Eagles and waterfowl 104 times from a vehicle slowly moving along a road adjacent to the reservoir.

We recorded the age class of each eagle observed. For this analysis, juvenile/immature birds (dark head), subadults (mottled head), and near-adults ("dirty" white head) were all grouped as subadults; only birds with completely white heads were considered adults. For each eagle observed, we noted its location, distance to water, perch type, and habitat. We also collected information on waterfowl distribution, noting the location, number and species of waterfowl observed. Location data were based on a 0.1 km scale following the river centerline.

We affixed radio transmitters to seven nesting adults (5 females, 2 males) and nine subadults of unknown natal origin. The radio-tagged adults included four nesting females at Britton Reservoir (nests 1, 3, 4, and 5). In the lower study area, we radiotagged the adult male at Nest 7 and both members of the pair at Nest 6. We mounted nine of the transmitters on retrices (Young 1983); the other seven were backpack-mounted, using teflon ribbons secured with cotton string over the carina. We captured eagles with either floating, noosed fish (Frenzel and Anthony 1982, Cain and Hodges 1989) or with padded leghold traps (Harmata 1985).

We used telemetry to locate and identify individual eagles during surveys. Telemetry monitoring sessions of radio-tagged adults were conducted by ground vehicle or boat throughout the morning hours in both breeding and non-breeding months. For analysis of relocation data within the study area, we considered only the first detection per day per location and excluded instances of soaring flight; we defined a relocation as a movement of at least 100 m. Outside the study area, we recorded the movements of radio tagged eagles on periodic aerial telemetry surveys around the northern California region.

From a boat and from the shoreline we observed eagles foraging in the reservoirs. A dirt road paralleling the river allowed access during tracking, although the forest canopy often obscured our view. We therefore constructed eight blinds along the forested river banks to allow observations of foraging in riverine habitat. We chose blind locations based on concurrent telemetry data and occupied several of them each morning. When a foraging attempt was observed, and after the eagle departed, we measured: 1) water depth, 2) substrate characteristics (e.g., cobble, sand, sediment), 3) surface turbulence (visually estimated), 4) water velocity (time for a floating object to travel 1 m), 5) stream habitat type (e.g., pool, run, riffle, see below), and 6) vegetation at the strike point. Even if the exact strike point could not be observed, certain data could be obtained if conditions such as depth and surface turbulence were homogeneous over wide areas. If possible, we visually identified the prey at the time it was taken, and also searched the foraging site later for prey remains.

Bald Eagle Diets. We determined diet by: 1) collecting prey items in and below nests and under perches, 2) observing foraging eagles, and 3) time-lapse photography. We identified prey remains by comparison with a reference collection of study area fishes, using scale keys (Casteel 1972, 1973), and by comparison with museum bird and mammal collections. Using bone length to fish length and fish length to weight equations empirically derived from fish captured during electrofishing (see below), we computed estimated total weights for non-duplicate prey items. By subtracting bone and scale weights (plus 5% total weight to account for inedible biomass) from fish weights in the prey reference collection, we obtained values of edible biomass. To calculate size and minimum number of fish in scale samples we determined scale age (Bagenal and Tesch 1978). We used standard weights for estimating non-fish prey biomass (Steenhof 1983, Dunning 1984).

We placed time-lapse movie cameras (Minolta Super-8 with intervolometers and light-activated switches) at three nests in 1983. These cameras, installed in boxes 3–5 m above nests, exposed one frame per 90 seconds during daylight.

Habitat Mapping. River habitat downstream from Britton Reservoir was mapped in 1984. The distribution of riverine habitats did not change with the flow releases under study (2.8–8.5 m^3/sec), but might change with spring run-off flows (>50 m^3/sec). Aerial photos and ground checking were used to classify river sections into the following categories: "Pools" are depressions in the streambed, with a major hydraulic control at the downstream end. Throughout most of the length and width of the pool habitat, current velocities are low relative to prevailing

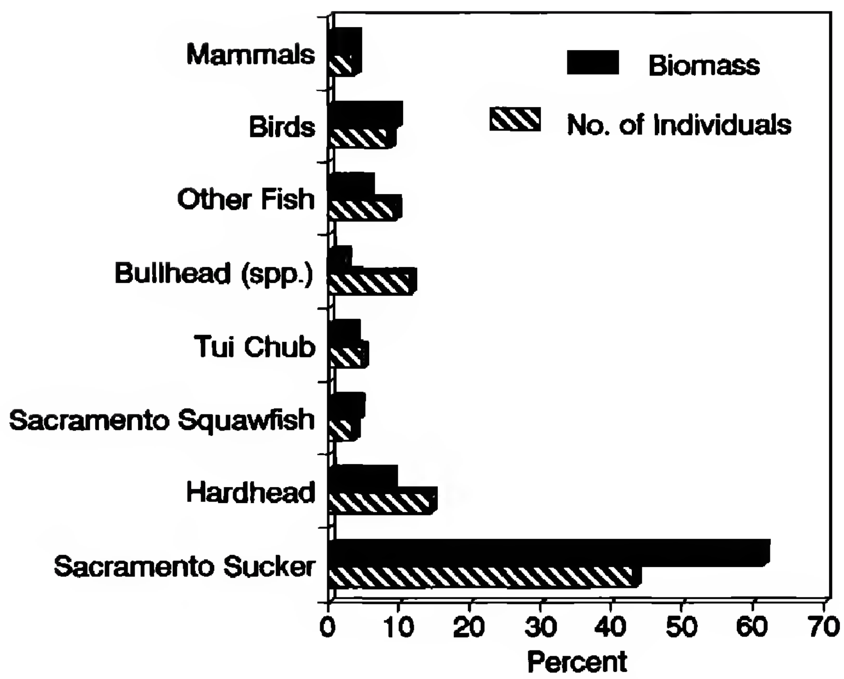

Figure 2. Diet of Bald Eagles in the Pit River study area as determined from a sample of 1166 prey items identified in remains (representing an estimated 938.1 kg of edible biomass).

streamflow. "Runs" are relatively deep, usually narrow channels. There is little or no white water in this habitat type and the hydraulic control is less distinct than in a pool; current velocity is relatively fast. "Riffles" are characterized by relatively shallow, fast-moving water flowing down gradients less steep than cascades and over substrates usually no larger than small boulders. "Cascades" are steep gradient white water with less than 10% quiet water. "Pocket water" usually contains boulders, with fast water liberally interspersed across the width of the stream. Pockets of quiet water (1–3 m in diameter) are frequent.

The principal river pools where eagles foraged were mapped on aerial photos and ground-checked in summer 1984. A digital planimeter was used to determine the area of various pool characteristics under normal summer flows and three experimental release flows. Assessment at each flow level included: 1) the presence and surface area of three water depth categories (less than 0.6 m (classified as "shallow"), 0.7–1.2 m, and over 1.3 m), 2) the presence or absence of surface turbulence (a rippling of the water surface that obscures visibility into the pool), 3) the estimated percentage of green algae or macrophyte coverage, 4) the total pool area, and 5) the length of the pool tail (the shallow area at the downstream end of the pool).

Prey Fish Distribution and Abundance in Reservoirs. Data on fish abundance and distribution in reservoirs were collected by gill netting, electroshocking, and carrion surveys. Vondracek et al. (1989) detailed the gill netting and electrofishing procedures. To summarize, gill nets were set monthly at either of two coves on Britton Reservoir using variable mesh gill nets set at surface (0–4 m), midwater (4–8 m), and bottom locations (8–16 m). We selected coves known to be eagle foraging areas. Nets were 36–38 m long and 1.5–1.8 m deep. Five nets at each depth were set for a minimum of 4 hr during all sampling periods. Variable mesh in equal-sized panels (3 m) ranged from 20–152 mm. The electrofishing surveys were conducted monthly at 27 stations on Britton Reservoir, although activities were suspended during the second Bald Eagle breeding season (March–July 1984) to avoid biasing Bald Eagle food habit data (electrofishing can kill fish and create a carrion food source for eagles). A Cofelt boat-mounted electrofisher was generally set at 350 volts DC and 60 pulses per second (Vondracek et al. 1989). Electrofishing stations were about 50 m in length and concentrated in shoreline locations. A diversity of shoreline habitats were electrofished, including shallow and deep water with various bottom substrates. Each captured fish was measured and weighed (to develop a length-weight regression relationship) and then released.

We surveyed carrion semi-monthly by boat 34 times on Britton Reservoir and 32 times on the three reservoirs in the lower study area. We used hoopnets to sample dead and injured fish emerging from powerhouse turbines at the inflow tailrace of Reservoir 4.

We compared the biomass and frequency of fish species in eagle prey remains at Britton Reservoir to the biomass and relative abundance of fish species in electrofishing samples and in surface (0–4 m) gill nets. We excluded fish from the comparison if they were less than the minimum size found as prey (250 mm for most species).

Prey Fish Distribution and Abundance in the River. Snorkeling surveys conducted in early summer and fall were used to determine fish abundance and distribution in the stream sections (see Baltz et al. 1987 for methods). Surveys were stratified by reach, river segment, and habitat, and were selected to cover various habitats within each stream section. Two to four snorkelers worked in an upstream direction starting below a selected habitat (see Baltz et al. 1987). Survey lengths were determined by habitat length and ranged from 25–150 m; 5–20 minutes were required to complete each survey. Seventy-three stream locations were surveyed four times each; data from 31 surveys were eliminated from the analysis because of poor visibility. Sampling area sizes were calculated from measurements of river lengths and widths. Each fish estimated to be over 50 mm SL (standard length: snout to base of tail) was recorded.

We obtained information on fish behavior from blinds above two pools in Reach 4 (July, August, and October of 1984) and from incidental observations. At half-hour intervals from 0600–1130 H, we identified, counted, estimated the size, and noted the location and activity of all fish visible in the pool. When visibility was low, we estimated overall fish activity by noting the number of rises during the observation period.

RESULTS

Eagle Occurrence in the Study Area. During the study period, paired eagles occupied eight nesting territories: five at Britton Reservoir and one each at reservoirs 4, 5, and 6 (Fig. 1). All nest sites were within 1 km of reservoirs. Only one was within 100 m of shore, and this nest was in the area least disturbed by humans. All nests but one were in mature Ponderosa Pines; Nest 8 was in a Douglas-fir (*Pseudotsuga menziesii*).

During our study, mated adults remained near

their nesting territories throughout the year. They generally laid eggs in late February and early March with young fledging in mid- to late June. The eight pairs fledged 17 young in 15 nesting attempts during the two years of study. Fledglings departed from the study area in late July or early August. We radiotracked five individuals on northward migrations apparently directed toward salmon runs in Canada or Alaska (Hunt et al. 1992b).

We observed the greatest number of eagles during January and February (13.5 birds per helicopter survey); subadults represented 37% of the total. During this time, subadult eagles were attracted to the powerhouse tailrace at Reservoir 4 where small fish from Britton Reservoir passed through the turbines and became available as carrion. Fewer eagles were observed along reservoirs and river sections in March and April when adults were incubating or perched near nests. In May, June, and July, 33% of all eagles were subadults. However, by early August, virtually all subadults had vacated the study area; they comprised only 5% of total sightings in September and October and 2% in November and December. All seven of the subadults radiotagged in winter later frequented the Klamath Basin 120 km to the north, and three subsequently returned to the study area.

Diet. Bald Eagles in the Pit River study area fed on a variety of prey species taken either alive or as carrion. Fish comprised 87%, birds 9%, and mammals 4% of the 1166 items in our samples (Fig. 2). Sacramento Sucker (*Catostomus occidentalis*) was the most important fish species (numbers of individuals and biomass) taken by eagles in all parts of the study area, followed by Hardhead (*Mylopharodon conocephalus*) and Sacramento Squawfish (*Ptychocheilus grandis*) (Table 1). Lower Britton Reservoir eagles utilized less suckers and more cyprinids—namely Hardhead, Tui Chub (*Gila bicolor*), and Sacramento Squawfish—than in the other regions.

Chi-square comparisons of prey remains data with those collected by time-lapse cameras at individual nests and in total (Table 2) did not suggest that larger species were over-represented in remains because of larger and more persistent bones (see Todd et al. 1982). The results also did not indicate that Tui Chub, a relatively delicate species, was underrepresented. Sample sizes for the time-lapse data were larger than for prey remains; some remains were likely dropped or taken from the nest by the eagles while other prey items may have been entirely consumed.

Of 17 species of birds identified in prey remains collected throughout the study area, all but 2 were waterbirds (Table 1). Birds were most numerous in prey samples collected in winter and spring and were absent in those obtained in July through October. Waterbird numbers in the study area were highest in winter and lowest in summer, but the number of species was highest (20) in spring. Canada Geese (*Branta canadensis*) were the most abundant (786 of 2608 bird records) and were present throughout the year. American Coots were the second most common (N = 576) but were observed only during fall and winter. Other common waterbirds were gull (*Larus* spp., N = 196), Common Merganser (*Mergus merganser*, N = 155), Double-crested Cormorant (*Phalacrocorax auritus*, N = 147), American Widgeon (*Anas americana*, N = 100), and Mallard (*Anas platyrhynchos*, N = 99). There was no significant association between numbers of the five most common waterbird species found in Bald Eagle prey remains and relative abundance of these five species recorded in waterbird surveys throughout the study area (Spearman rho = 0.20, $P > 0.05$).

Foraging on Britton Reservoir. The five pairs of bald eagles nesting on Britton Reservoir foraged in all portions of the reservoir, but rarely visited the river sections upstream or downstream. The linear ranges along the reservoir of three radio-tagged adult females were 0.7, 2.4, and 2.7 km. Although we radiotagged no breeding male eagles on Britton Reservoir, visual observations suggested that their foraging ranges were similar to those of the radiotagged females.

The eagles foraged on carrion and moribund fish, as well as live prey. We observed 42 forage attempts (52% successful) including 22 (52%) in open water or flowing reservoir habitat, 17 (41%) in cove, backwater, shallow gravel bar, or marsh habitat; 3 (7%) were piracies from Osprey (*Pandion haliaetus*) and Great Blue Heron (*Ardea herodias*). Prey taken were fish (N = 22), namely Sacramento Sucker, Carp (*Cyprinus carpio*), Hardhead, and small fish, probably Tule Perch (*Hysterocarpus traski*). At least 8 fish (36%) were taken as carrion.

Eagles flying out from shore over deep water took carrion fish or attacked fish swimming at or near the surface. Alternatively, eagles foraged in reservoir shallows, particularly in coves where they launched their attacks at live fish from perches. Fish spawned in and around the mouths of tributaries in coves where the clear inflow of springs and creeks in-

Table 1. Number and edible biomass of fishes, birds and mammals found in Bald Eagle prey remains in five subunits of the Pit River study area. Remains were collected in and below nests and from below perches, during all seasons.

	Britton Reservoir				Lower Study Area					
	Upper Nests 1, 2		Lower Nests 3, 4, 5		Reservoir 4 Nest 6		Reservoir 5 Nest 7		Reservoir 6 Nest 8	
	No. (%)	% Biomass	No. (%)	% Biomass	No. (%)	% Biomass	No. (%)	% Biomass	No. (%)	% Biomass
Fish										
Sacramento Sucker	284 (52.3)	72.8	84 (24.9)	44.9	80 (51.0)	60.2	32 (38.1)	32.2	24 (54.6)	68.5
Bullhead sp.	84 (15.5)	3.1	39 (11.5)	2.0	4 (2.5)	2.0	6 (7.1)	0.2	3 (6.8)	0.4
Hardhead	63 (11.6)	7.2	66 (19.5)	14.3	24 (15.3)	7.6	9 (10.7)	6.2	6 (13.6)	8.8
Tui Chub	21 (3.9)	2.6	30 (8.9)	8.2	5 (3.2)	2.9	0 (0.0)	0.0	0 (0.0)	0.0
Sacramento Squawfish	19 (3.5)	3.6	17 (5.0)	6.6	6 (3.8)	5.9	1 (1.2)	0.7	1 (2.3)	1.6
Other[a]	25 (4.6)	3.3	61 (18.1)	11.6	17 (10.8)	6.2	6 (7.2)	4.5	1 (2.3)	0.4
Total (% of total)	496 (91.4)	92.6	297 (87.9)	87.6	136 (86.6)	84.8	54 (64.3)	43.8	35 (79.6)	79.7
Birds[b] (% of total)	30 (5.5)	4.9	29 (8.6)	8.5	14 (8.9)	11.2	26 (30.9)	46.3	3 (6.8)	7.2
Mammals[c] (% of total)	17 (3.1)	2.5	12 (3.5)	3.9	7 (4.5)	4.0	4 (4.8)	9.9	6 (13.6)	13.1

[a] Other fish species (and total number of occurrences) included: 8 Channel Catfish (*Ictalurus punctatus*), 8 Carp, 38 minnows (Cyprinidae sp.), 24 crappie (*Pomoxis* sp.), 14 Tule Perch, 3 Rainbow Trout, 7 trout (*Salmo* sp.), 6 Largemouth Bass, and 2 sunfish (Centrarchidae sp.)

[b] Birds included: 29 American Coot (*Fulica americana*), 18 Dabbling ducks (*Anas* spp.), 11 Mallard, 10 geese (Anserinae), 8 grebes (Podicipedidae), 6 Tundra Swan, 5 Common Merganser (*Mergus merganser*), 4 unidentified birds, 3 Ruddy Duck (*Oxyura jamaicensis*), 2 Great Blue Heron, 2 gull (*Larus* sp.), 1 Double-crested Cormorant, 1 Common Goldeneye (*Bucephala aclangula*), 1 Ring-necked Pheasant (*Phasianus colchicus*), and 1 Screech Owl (*Otis kennicottii*).

[c] Mammals included: 12 Muskrat (*Ondatra zibethica*), 8 California Ground Squirrel (*Citellus beecheyi*), 7 Western Gray Squirrel (*Sciurus griseus*), 5 rabbits (Leporidae), 5 unidentified squirrels (Sciuridae), 3 Black-tailed Deer (*Odocoileus hemionus*), 2 Mountain Beaver (*Aplodontia rufa*), 2 Domestic Cow (*Bovus domesticus*), 1 Yellow-bellied Marmot (*Marmota flaviventris*), and 1 Striped Skunk (*Mephitis mephitis*).

creased fish visibility to eagles in the otherwise turbid reservoir.

We occasionally observed bottom feeders such as sucker and catfish swimming slowly near the surface of Britton Reservoir. Surface gill netting and hydroacoustic surveys indicated that frequency and diversity of fish swimming near the surface were greatest at dusk, intermediate at dawn, and lowest at midday, and that fish were most abundant near the surface during the warmer months (Vondracek et al. 1989). During the nesting season, Bald Eagle foraging occurred mostly in the morning. Of 236 prey deliveries recorded by time-lapse cameras at three nests (Nests 5, 6, and 8) totaling 98 camera-days, 49.6% occurred between 0600–1100 H, 29.2% between 1100–1600 H, and 21.2% occurred between 1600–2100 H.

Fish carrion was available on Britton Reservoir in late spring and early summer. In June and July, we found 12.9 items per survey (range = 3–30) compared with 1.7 items per survey from August through May (range = 1–6). Sacramento Sucker and Tule Perch represented 57% and 35%, respectively, of 99 carrion fish found in the June–July surveys. Many of these fish had apparently died from spawning stress, and some of the Tule Perch counted in the surveys were still alive, floating moribund at the surface on their sides. Some Sacramento Squawfish and Hardhead were killed by anglers. We were unable to determine whether significant numbers of dead fish were stranded during reservoir level fluctuations, but we occasionally found dead suckers along flat, grassy shorelines of Britton Reservoir and other backwaters in the study area.

Fish Abundance Versus Eagle Diet at Britton Reservoir. Sacramento Sucker comprised only 11% of the number of fish in electrofishing samples on Britton Reservoir, but because of their large size

Table 2. Number and biomass of fish species identified in the Pit River study area by time-lapse photography and prey remains collected over the same periods, Nest 5 from 23 May to 3 July, Nest 6 from 29 May to 30 June, and Nest 8 from 11 June to 5 July.

	Nest 5[a]				Nest 6[b]				Nest 8[c]			
	Remains		Time-Lapse		Remains		Time-Lapse		Remains		Time-Lapse	
Species	No.	Biomass (g)	No.	Biomass (g)	No.	Biomass (g)	No.	Biomass (g)	No.	Biomass (g)	No.	Biomass (g)
Sac. Sucker	6 (23.1%)	6406 (43.1%)	14 (26.4%)	7049 (32.1%)	11 (52.4%)	9010 (72.1%)	24 (82.9%)	15 995 (88.7%)	15 (88.2%)	9558 (92.8%)	28 (80.0%)	12 731 (84.3%)
Hardhead	11 (42.3%)	5258 (35.4%)	11 (20.8%)	4685 (21.3%)	2 (9.5%)	838 (6.7%)	1 (3.4%)	369 (2.0%)	2 (11.8%)	738 (7.2%)	4 (11.4%)	1565 (10.4%)
Tui Chub	2 (7.7%)	1375 (9.3%)	9 (17.0%)	6137 (27.9%)	1 (4.8%)	471 (3.8%)	1 (3.4%)	732 (4.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Cyprinid spp.	1 (3.8%)	369 (2.5%)	6 (11.3%)	2385 (10.9%)	2 (9.5%)	1249 (10.0%)	1 (3.4%)	165 (0.9%)	0 (0.0%)	0 (0.0%)	3 (8.6%)	805 (5.3%)
Other	6 (23.1%)	1436 (9.7%)	13 (24.5%)	1708 (7.8%)	5 (23.8%)	927 (7.4%)	2 (6.9%)	774 (4.3%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Total[d]	26	14 844	53	21 964	21	12 495	29	18 035	17	10 296	35	15 101

[a] $\chi^2 = 5.18$, df = 4, $P = 0.27$.
[b] $\chi^2 = 5.65$, df = 4, $P = 0.23$.
[c] $\chi^2 = 1.55$, df = 2, $P = 0.46$.
[d] $\chi^2 = 4.88$, df = 4, $P = 0.30$.

Table 3. Number and percent of the seven most abundant fish species collected in Lake Britton by electrofishing and surface gill netting.

	Electrofishing				Surface Gill Netting	
	No.	%	Biomass (g)	%	No.	%
Tule Perch (*Hysterocarpus traski*)[a]	2130	38.8	25 705	3.6	27	12.0
Hardhead (*Mylopharodon conocephalus*)[a]	1120	20.4	80 921	11.2	125	55.6
Sacramento Sucker (*Catostomus occidentalis*)[a]	605	11.0	452 884	62.6	33	14.7
Sacramento Squawfish (*Ptychocheilus grandis*)[a]	588	10.7	68 796	9.5	19	8.4
Black Crappie (*Pomoxis nigromaculatus*)[b]	457	8.3	24 398	3.4	20	8.9
Bluegill (*Lepomis macrochirus*)[b]	322	5.9	3 614	0.5	0	0
Largemouth Bass (*Micropterus salmoides*)[b]	269	4.9	66 561	9.2	1	0.4
Total	5491	100.0	722 879	100.0	225	100.0

[a] Native species.
[b] Introduced species.

represented over 60% of the total biomass (Table 3). Sacramento Sucker, Hardhead, and Sacramento Squawfish together accounted for over 80% of the total fish biomass. Tule Perch, the most numerically abundant fish, comprised only 3.6% of the biomass samples. In the gill netting sample, suckers represented over 80% of the biomass.

Eagle prey selection at Britton Reservoir was significantly associated with fish abundance as indicated by gill netting data (Spearman rho = 0.626; $P < 0.05$) but not electrofishing data (Spearman rho = 0.191; $P < 0.10$). Ictalurids and Tui Chub were well represented in the eagles' diet but were rare in the electrofishing surveys (Vondracek et al. 1989). Conversely, Tule Perch, Largemouth Bass (*Micropterus salmoides*), and other centrarchids were abundant in the electrofishing surveys, but relatively unimportant to eagles. The relative percent of biomass of Hardhead and sucker in the diet was very similar to that in electrofishing; sucker and Hardhead comprised 73.8% of the 723 kg of fish sampled by electrofishing (Table 3) and averaged 73.5% of the eagles' diet.

Eagles nesting on the downstream portion of Britton Reservoir took fewer Sacramento Suckers than eagles nesting on the upstream section (Table 1). To evaluate the difference, we compared the relative abundance of Sacramento Sucker >200 mm, collected by electrofishing in upper and lower Britton Reservoir. We found that the upstream section contained more Sacramento Sucker >200 mm (19.1 per station; Vondracek et al. 1989) than the lower part of the reservoir (8.5 per station) where eagles relied more heavily on other species.

Foraging on the Small Reservoirs. Eagles nesting near the small downstream reservoirs took live fish and carrion fish (and waterfowl) in the reservoir bodies and inflow areas and dead and moribund fish emanating from the turbines of powerhouses situated on the reservoirs. Sacramento Sucker were the most abundant fish species both in terms of numbers and biomass identified in the downstream reservoirs (Reservoirs 4, 5, and 6) during electroshocking surveys. Hardhead, Sacramento Squawfish, and Tule Perch were also common. We saw eagles attempt to catch Hardhead and sucker near shore and in the main

Table 4. Habitat use by radio-tagged adult Bald Eagles nesting near riverine habitat as determined by radio-telemetry locations. Data include only the first detection of the day per location and exclude instances of soaring flight.

Territory	Sex	Reach 3	Reservoir 4	Reach 4	Reservoir 5	Reach 5	Tunnel Reservoir	Total Detections
Nest 7	Male	—	—	114 (17.2%)	271 (40.9%)	236 (35.7%)	41 (6.2%)	662
Nest 6	Male	1 (0.4%)	142 (64.3%)	78 (35.3%)	—	—	—	221
Nest 6	Female	0 (0.0%)	20 (38.5%)	32 (61.5%)	—	—	—	52

channels of reservoirs 4 and 5. At the upstream end of Reservoir 4, we frequently observed adults (Nest 6) taking suckers in the spring and summer in the currented shallows of an island gravel bar at the reservoir inflow where suckers were spawning. A backwater inlet at Reservoir 5 stranded several suckers on at least one occasion when water levels dropped.

We quantified habitat characteristics for 50 foraging attempts (60% successful) on the downstream reservoirs. Of these, 27 (54%) occurred in open water or flowing reservoir habitat, 13 (26%) in backwaters or marshes, 9 (18%) in powerhouse tailrace waters, and 1 (2%) unknown. Fourteen of 30 prey items appeared to be carrion. Tule Perch and crappie (*Pomoxis* sp.) carrion emerged from the powerhouse tailrace at Reservoir 4 primarily during winter and spring. Peaks in small carrion fish emerging from the tailrace into the reservoir corresponded with increased eagle attendance near the tailrace.

Bald Eagle Use of the River Sections. Bald Eagles that nested near the small reservoirs in the lower study area frequently perched and hunted along the river sections. In over half of 662 telemetry relocations of the radio-tagged adult male from Nest 7 (August 1983–February 1984 and May–December 1984) the eagle was in riverine habitats upstream and downstream of Reservoir 5 (Table 4). The total range was 22 river km.

Similarly, 35.7% of recorded relocations by the radio-tagged male at Nest 6 (6 June to 10 December 1984) were on the river rather than the reservoir. During 9 August to 30 September 1983, his mate perched mainly in riverine habitat (61.5% of relocations). Figure 3 shows that the ranges of the pair of radio-tagged adults at Nest 6 were very similar, both in extent (ca. 11 km) and distribution. Although the upstream river section (Reach 3) was just as accessible to the pair as the downstream reach (Reach 4), we observed the male in Reach 3 only once and

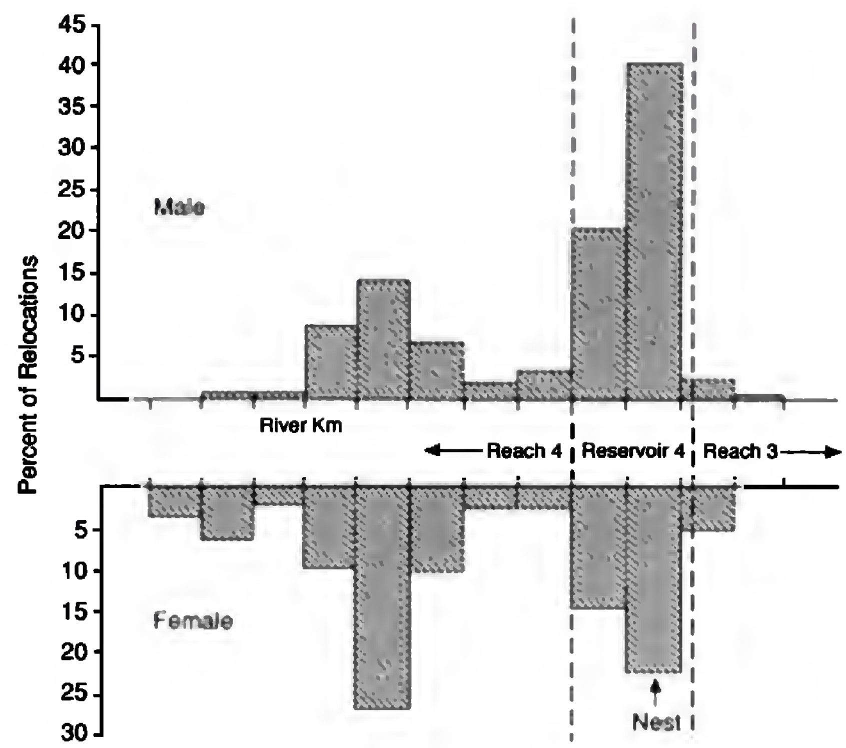

Figure 3. Home ranges of the adult pair of Bald Eagles at Nest 6 in the Pit River study as revealed by radiotelemetry.

Table 5. Mean number and biomass per hectare of the two major Bald Eagle prey species recorded in three riverine habitats on snorkel surveys of the Pit River in 1983 and 1984.

		HARDHEAD			SACRAMENTO SUCKER		
	NO. OF SURVEYS	NO.	BIOMASS (kg)	MEAN SIZE (g)	NO.	BIOMASS (kg)	MEAN SIZE (g)
Reach 3							
Pool	45	135.8	47.2	(347.6)	102.5	29.2	(284.9)
Run	40	7.1	2.1	(295.7)	345.5	23.0	(66.6)
Riffle	26	0.9	0.3	(333.3)	142.8	13.5	(94.5)
Reach 4							
Pool	12	57.8	23.2	(401.3)	138.0	100.9	(731.2)
Run	32	33.0	13.0	(393.9)	352.2	227.8	(646.8)
Riffle	25	12.9	2.0	(155.0)	443.2	279.5	(630.6)
Reach 5							
Pool	18	26.5	2.8	(105.7)	180.7	62.7	(346.9)
Run	34	55.6	12.4	(223.0)	447.0	133.6	(298.9)
Riffle	29	21.8	5.1	(233.9)	475.5	134.2	(282.2)

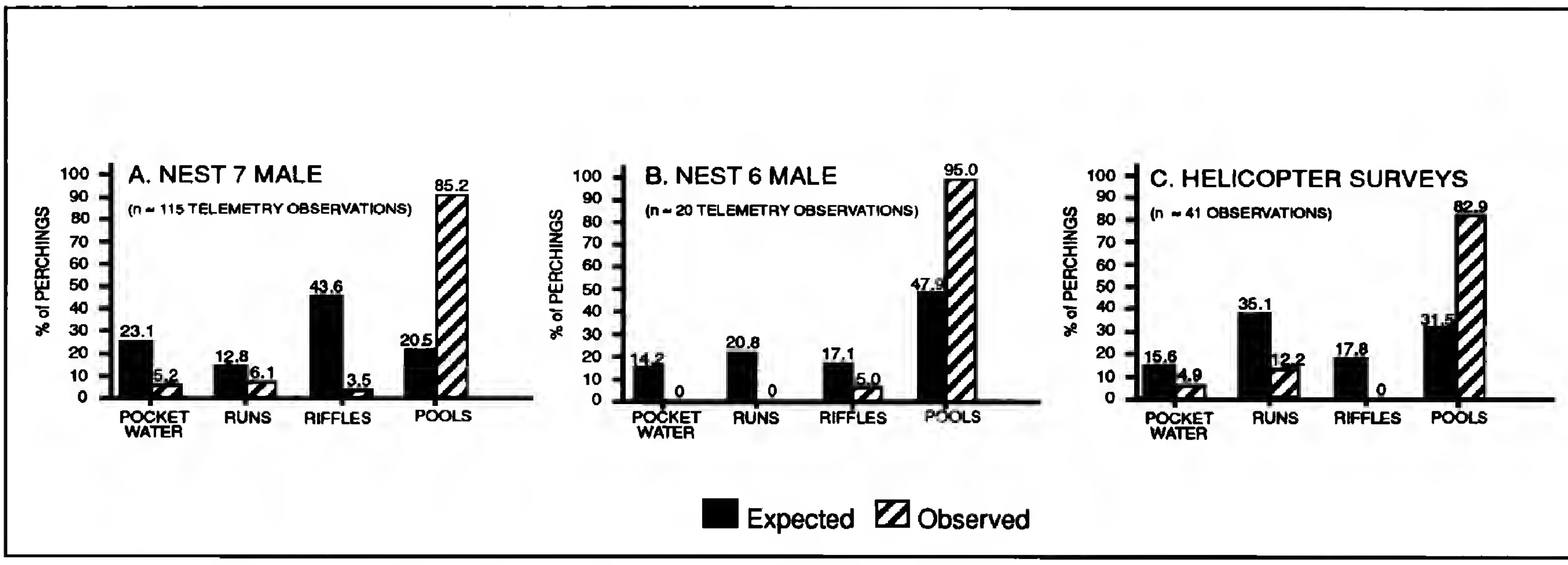

Figure 4. Observed and expected utilization of riverine habitats by Bald Eagles in Reaches 4 and 5. Graphs A and B show the expected percentages of telemetry observations of perchings in riverine habitats based on the proportional occurrence of each habitat within the home range of the eagle. For observations during helicopter surveys (C), percentages are based on habitat availability throughout Reaches 4 and 5.

the female never. In Reach 4 the ranges of the Nest 6 pair overlapped only slightly with that of the Nest 7 male.

Fish Occurrence in the River Reaches. Snorkeling surveys on the three river reaches (3, 4, and 5) provided data on the occurrence of Sacramento Sucker, Hardhead, Sacramento Squawfish, and Rainbow Trout (*Oncorhynchus mykiss*). Table 5 presents mean number and biomass per ha for sucker and Hardhead identified in the snorkeling surveys. Suckers were large and numerous in the riffles and runs of Reach 4, equally plentiful but smaller in Reach 5, and very small and least frequent in Reach 3. Conversely, Hardhead numbers were highest in Reach 3 pools, although they appeared larger in Reach 4. Trout numbers followed a similar pattern to Hardhead; they were more numerous in Reach 3 (especially riffles), intermediate in Reach 4, and fewest in Reach 5. Squawfish were most abundant in Reach 5 and intermediate in the other reaches; however, their numbers and biomass were comparatively low. We will later show an apparent connection between the distribution of these fishes, namely suckers, and the occurrence of foraging eagles.

Fish Behavior in the River Reaches. Our observations of fish behavior in Reach 4 showed that both Sacramento Sucker and Hardhead exhibited activity peaks during the morning. Suckers spent most of their active period slowly grazing on algae-covered cobble substrate. It was apparent that as they moved into the shallow areas (tails) of pools they came close enough to the surface to be caught by eagles. Their movement into pool tails may have also been related to spawning. Sacramento Suckers typically spawn in riffles (Moyle 1976), and in our study area riffles are usually preceded by pools. Therefore, suckers may pass though pool tails on their way to and from spawning areas.

Hardhead activity was variable. These sight feeders hovered in the middle of the water column and cruised along the river bank. We observed Hardhead feeding at the surface and in aquatic vegetation, browsing on the bottom, and apparently feeding on invertebrate drift in the water column. On two occasions, we observed eagles capture Hardhead swimming around beds of rooted aquatic vegetation. Hardhead feeding in this manner appeared to have their heads obscured by the plant material and appeared unaware of the eagle attack.

Riverine Habitat Selection. The riverine habitats used by the two radio-tracked male eagles (Nests 7 and 6) differed significantly from the proportional occurrence of aquatic habitats within their home ranges (Fig. 4). From 115 telemetry observations of the Nest 7 male, we recorded significantly more occurrences ($N = 98$, 85.2%) on river pool habitat than expected by chance ($\chi^2 = 297$, df = 3, $P < 0.001$). Similarly, in 20 river habitat observations of the Nest 6 male, he chose pools ($N = 19$, 95%) more often than expected by chance ($\chi^2 = 18.5$, $P < 0.001$). Helicopter surveys also showed eagles selecting pools disproportionately to pool occurrence ($\chi^2 = 94.9$, $P < 0.001$, 83% use in 34 of 41 observations compared to 31% availability; Fig. 4).

Foraging Behavior at River Pools. From blinds situated at riverine pools we noted that eagle attacks typically began high above the water from tree perches (20 of 25 observations); only one eagle struck without perching first. Attack distances ranged from 10 to 75 m. The success rate for all riverine forages observed from blinds was 16 in 25 attempts (64%), with 1 outcome undetermined. Exposed boulders were used as sites to drag and eat large fish. We identified the prey taken in ten instances: eight were Sacramento Sucker and two were Hardhead.

Water depth ranged from 0.1–1.26 m at 15 foraging strike points. Of 17 assessments of surface conditions in strike areas, only 2 showed a disturbance greater than swirls, whereas 11 had a glassy surface. The bottom was visible in 17 of 18 measurements of strike point turbidity; the exception showed visibility to a depth of 0.4 m. Water velocity at strike points was usually low; 7 of 16 observations showed no measurable current.

An analysis of river pool habitat characteristics and prey distribution at 11 pools indicated that eagle occurrence (total number of visits by telemetered eagles and eagles observed in helicopter surveys) was positively associated with the number of prey-sized fish per 100 m^2 (as determined by the snorkeling surveys, Pearson correlation coefficient, $r = 0.77$, $P < 0.01$). We also found a significant positive correlation of eagle occurrence with percent of pool area classified as "smooth/shallow" (no surface turbulence and <0.6 m deep, Pearson $r = 0.67$, $P < 0.03$). Comparisons of eagle occurrence with pool area, maximum depth of pool, percent algae coverage, length of pool tail (as a percent of pool length), and the total estimated number of prey fish per pool were not significant.

An experimental increase in flow above summertime conditions (4.2 m^3/sec) reduced the amount of shallow areas of no surface turbulence. The loss of smooth/shallow habitat for Reach 4 was quite high, with decreases for all seven pools averaging over 50% (minimum 27.6%, maximum 100%) at 8.5 m^3/sec flow. Water velocity in the studied pools generally increased with greater flows, but changes within smooth/shallow areas were inconsistent, with velocities both increasing and decreasing. Decreases in areas of no surface turbulence also resulted at each of the three pools measured in Reach 5 (minimum 7.2%, maximum 54.3%) when flows were increased from 2.8–4.2 m^3/sec.

Increased flows did not widen the river at most pools because of the relatively steep-sided canyon; therefore, availability of tree perches was not affected. Because pool length was dictated by hydraulic factors and did not change with flows, perch positions relative to pool boundaries did not change. However, increased flow reduced the number of exposed boulders at water level, which are often important to Bald Eagles as perches for manipulating heavy prey.

We caution the reader that specific management implications suggested by these results (i.e., managing for smooth/shallow habitat) may not apply to other river systems where Bald Eagles forage. Differing hydrologic and biotic factors may diversely influence the occurrence of catostomids and other prey fishes in pools, their activities within them, and their vulnerability to eagle attack. In Arizona, Hunt et al. (1992c) found pools least favored among the riverine habitats where Bald Eagles foraged on Desert Sucker (*Catostomus clarki*), Sonora Sucker (*C. insignis*), and Carp.

Eagle Distribution Versus Prey Occurrence. Based on the number of Bald Eagle sightings during helicopter surveys and the number and biomass of sucker per ha for six river segments (each river reach divided into upper and lower segments), eagle preference for the different river reaches was likely associated with the abundance of large suckers. The total number of eagle sightings in helicopter surveys were 1 and 5 for lower and upper Reach 3, respectively, and 24 for upper Reach 4. We saw eagles 15–18 times in each of the remaining segments.

The segments with the lowest eagle sightings also were estimated to have the lowest sucker populations (32.2 and 1.4 sucker per ha for lower and upper Reach 3, respectively). Upper Reach 4 had the largest sucker population (388.7/ha), the highest biomass (286.9 kg/ha) and the highest number of eagle sightings. The value for Spearman's rank correlation representing the correspondence between number of eagle sightings and biomass of suckers was 0.89 ($P < 0.05$). There was no significant correlation with numbers of suckers (rho = 0.77).

We reported above that the telemetered nesting pair of eagles at Reservoir 4 often foraged in the river section downstream of the reservoir (Reach 4), but rarely ventured upstream to the equally accessible Reach 3. Although suckers in size categories taken by these eagles (200–450 mm) were found in all habitats during snorkeling surveys of Reach 4 and electrofishing surveys of Reservoir 4, there were

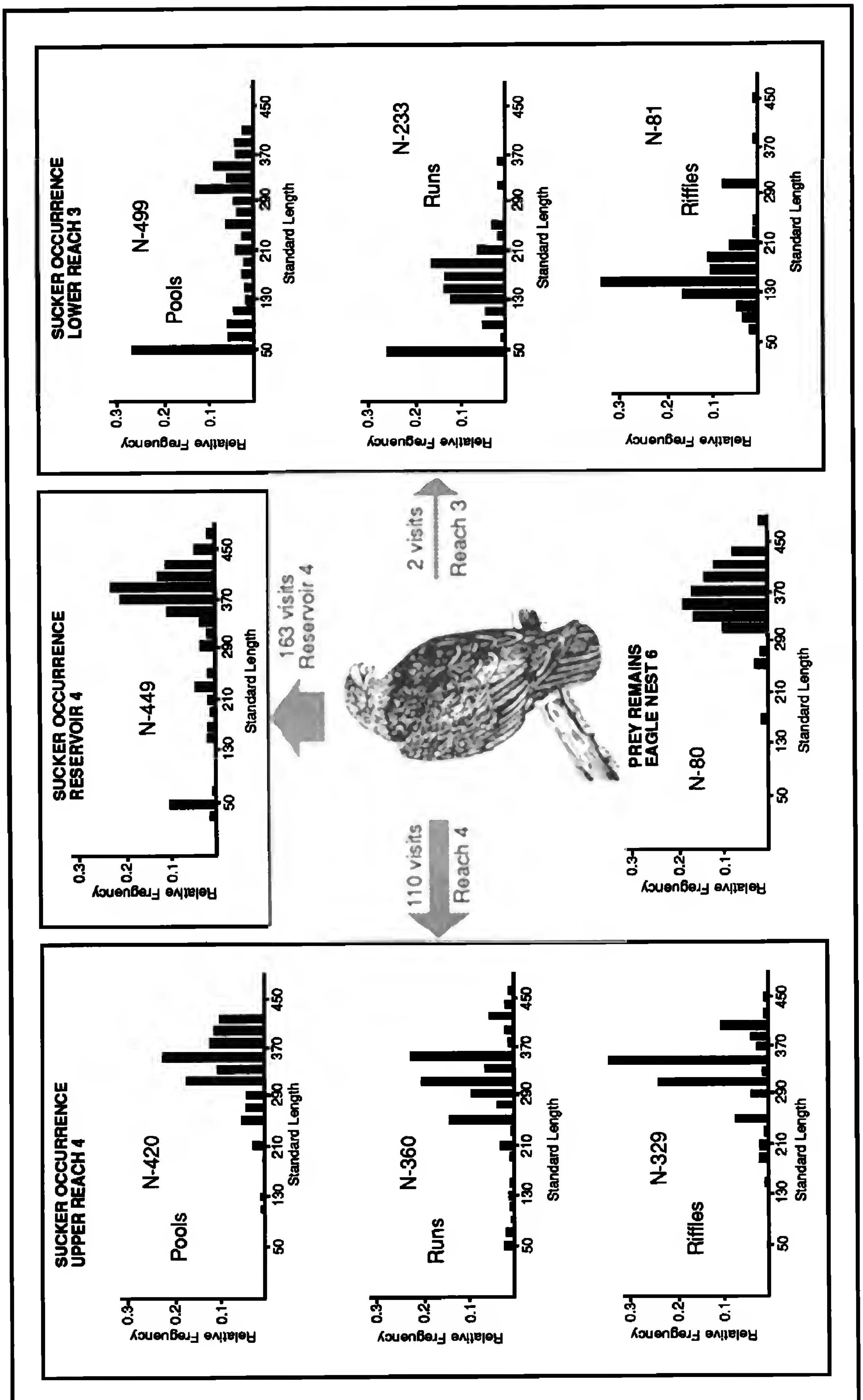

Figure 5. Relative length-frequency distributions of Sacramento Sucker in prey remains from Nest 6 compared with sucker length-frequencies observed in fish population surveys.

relatively few such fish observed in Reach 3 where smaller suckers were numerous (Fig. 5). Pools in upper Reach 4 contained four times the biomass of sucker per unit area (176.5 kg/ha) as lower Reach 3 pools (44.4 kg/ha). Sucker growth was limited in Reach 3 probably because of reduced algae growth and colder water than is optimum for suckers. Because of the diversion tunnel to the downstream powerhouse, Reach 3 was the only reach that did not receive relatively warm, nutrient-rich reservoir water in summertime.

DISCUSSION

Several points suggest a simple relationship between relative prey species abundance and prey selection. These points include the dominance of Sacramento Sucker in eagle diets in all parts of the study area, the increased use of other species in Lower Britton Reservoir where suckers were less common, the disproportionate use of pools with the highest densities of prey fish, and the rarity of eagle visits to Reach 3 where Sacramento Sucker of appropriate body size were in relatively low density.

Our data also show how prey behavior and life history can influence vulnerability to predation. Sacramento Sucker were not only numerous, they were also vulnerable to eagles in more ways than other species. They became available when they: 1) foraged in shallow water, 2) spawned in shallows, and 3) appeared as carrion. The first two components of vulnerability, characteristic of many catostomids, no doubt account for their occurrence in the diets of Bald Eagles over much of their inland range (Dunstan and Harper 1975, Todd et al. 1982, Swenson et al. 1986, Haywood and Ohmart 1986, Gerrard and Bortolotti 1988, Hunt et al. 1992c). Not only do suckers typically enter shallow water to spawn and graze (photosynthesis is highest in shallow habitats), but their downward visual orientation must leave them more vulnerable to eagle attack than sight-feeding fish (see Swenson 1979, Todd et al. 1982 for discussion). This point helps to explain the apparent contradiction of a bottom-feeding fish being the major prey of a surface-feeding predator (Haywood and Ohmart 1986). Accordingly, sight-feeding cyprinids (Hardhead and Sacramento Squawfish) appeared in significantly less frequency in prey remains than predicted by their occurrence relative to Sacramento Sucker in the gill netting and electroshocking samples on Britton Reservoir (Tables 1 and 3). Trout, also sight-feeders, were common in the river reaches, but were rarely taken by eagles. Both Hardhead and trout often wait near the surface for insects, but these fish tend to be oriented upward and are more aware than suckers of any movement above them.

We believe the timing and occurrence of sucker mortalities on Britton Reservoir may contribute to the unusually high nesting density of Bald Eagles there. This carrion "bloom" coincides with the second half of the nestling cycle, including the post-fledging period. Large post-spawning dieoffs are atypical among catostomids, and P.B. Moyle (pers. comm.) believes that the proportion of the total sucker spawners dying each year as a result of spawning stress is small. However, dead and dying fish, drifting down from the relatively long river reach upstream, tend to accumulate in the reservoir inflow area where they are highly visible to the eagles. Carrion fish may also be produced by stranding as a result of flow variation from the powerhouse upstream of the reservoir.

Another point of difference between eagle diet and species occurrence in the fisheries inventories involved ictalurids. Bullheads (*Ictalurus melas* or *I. nebulosus*) were absent in the extensive electrofishing, gill netting, and carrion survey samples on Britton Reservoir, and yet we identified 123 individuals in eagle prey remains (Table 1). Dunstan and Harper (1975) and Van Daele and Van Daele (1982) mention that bullheads often swim or "bask" near the surface, and indeed, we witnessed unidentified ictalurids doing so on Britton Reservoir. How they avoided the gill nets is unknown to us.

Finally, although relative eagle use of the three river reaches was directly related to the abundance of large suckers (>200 mm), our data show that physical conditions promoting prey vulnerability were more important in attracting foraging eagles to specific habitats than were factors influencing prey density. Eagles chose river pool habitat despite the fact that sucker densities in Reaches 4 and 5 were invariably lower in pools than in runs or riffles, and there were no consistent size-class differences of suckers between the three habitats (Table 5).

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Short Communications

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Increased Parental Care in a Widowed Male Marsh Harrier (*Circus aeruginosus*)

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Pair bonding and distribution of functions is essential to the successful breeding of birds (Trivers 1972). This is especially important in raptors, where food is generally not abundant and its capture requires a considerable hunting effort (Newton 1979). Besides food supply, parental care involves more activity including: protection of chicks from inclement weather and predators, nest maintenance and sanitation, and territorial defense (Johannesson 1975, Newton 1986, Fernández 1992), which require much time and energy and can hardly be carried out by a single parent.

In the spring of 1990, during the study of several nests of Marsh Harriers (*Circus aeruginosus*), we noted the disappearance of one of the breeding females. Hence, we had the opportunity to see to what extent the loss of his mate affected the parental behavior of the widowed male and compare his behavior with that of other neighboring breeding pairs.

Methods

The study was carried out at the Dos Reinos wetland (Ebro Valley, Spain), where ten monogamous pairs of Marsh Harriers bred in 1990 (Fernández 1990). Two of the nests failed during incubation. The other eight breeding pairs were observed from a hide about 300–500 m from the nests. We recorded separately for each sex the time spent by adults in the nest area (limits of wetland area), food items supplied to nestlings, territorial chases and other aspects of parental care (Fernández 1992). To estimate the breeding stages, chicks were aged according to body development (body mass, tarsus length and 6th primary length; Altenburg et al. 1987, González 1991).

During our study we observed the disappearance, for unknown reasons, of the hen in one pair. The disappearance occurred on 20 June 1990 when the chicks were 37–38 d old. A week before, two chicks had been observed in the nest but whether the loss of one young was caused by the female's disappearance or happened previously is not certain. The chick that survived flew when 43 d old, within the usual range of first flight times in the Marsh Harrier (Cramp and Simmons 1980).

The behavior of the male before female loss had been studied over 4 d for 28 hr. Following the disappearance of the female, the behavior of its mate was monitored for 3 d (a total of 22 hr), until the only surviving chick flew. Three aspects of the behavior of the widowed male (percent time spent in nest area, number of food items delivered per hour and number of territorial chases per hour) were compared to those of neighboring pairs over the same breeding period. Observations of neighboring pairs occurred on 20 d (120 hr) before loss and on 16 d (108 hr) during the last days before flying. Statistical comparisons between hours with and without chases and prey delivered were made by means of χ^2-tests in 2 × 2 contingency tables (Sokal and Rohlf 1969).

Results

As shown in Table 1, the input of parental care by the widowed male before the loss of his mate was similar to input of other males. He spent only slightly more time in nest area than neighboring males ($\chi^2 = 1.07$, $P > 0.05$), delivered a few less food items to nestlings ($\chi^2 = 1.39$, $P > 0.05$) and defended his nesting area as much as other males ($\chi^2 = 0.03$, $P > 0.05$).

After female loss (Table 1) the widowed male: a) spent significantly more time in the nesting area than neighboring males in the same nestling period ($\chi^2 = 103.02$, $P < 0.001$) and about the same proportion of the time as females, b) supplied slightly more food items per hour than mated males ($\chi^2 = 1.75$, $P > 0.05$) though significantly fewer than males and females together ($\chi^2 = 3.91$, $P < 0.05$), and c) defended his nesting area more frequently than other males ($\chi^2 = 6.20$, $P < 0.05$) though not more frequently than mated birds taken together. The number of chases in relation to time spent in nesting area was, however, similar for the single male (1.34 chases/hr) and other male birds (1.58 chases/hr).

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Table 1. Comparison of parental care of a widowed male Marsh Harrier with neighboring paired males, before and after female loss in the Ebro Valley, Spain.

	Before Loss		After Female Loss		
	Widowed Male	Paired Males	Widowed Male	Paired Males	Male and Female Combined
Observation time (hr)	28	120	22	108	108
% time in nest area	22.5	14.5	33.9	12.6	36.4
Food items/hr	0.39	0.51	0.64	0.48	0.82
Defense chases/hr	0.25	0.27	0.46	0.20	0.51

Discussion

Disappearance of one of the parents during breeding is not uncommon among birds of prey (Newton 1979). In most cases, if the lost mate is not rapidly replaced, abandonment of the nest results (Newton 1976). Occasionally, however, especially if the death of a parent occurs toward the end of the nestling period (Newton 1986), the remaining adult can successfully rear young. Such has been reported previously for several raptors, including Marsh Harrier (Cramp and Simmons 1980). Successful single-parent broods must likely involve a greater parental effort (Trivers 1972) by the remaining bird or a reduction in number or quality of fledglings. Our observations indicate that the male Marsh Harrier widowed at the late nestling stage of the breeding season made a greater parental effort than mated males, at least in several facets of parental care. He spent more time in the nesting area, delivered a few more (although not significantly more) food items to nest, and carried out more territorial defenses. The increase in number of chases was probably related to the greater amount of time spent in the nesting area. Sasvari (1990) has found experimentally that in the Great Tit (*Parus major*) widowed birds fed nestlings more frequently than either of the mated parents but less than both together, as was also the case with the Marsh Harrier we studied.

Our results suggest that male harriers are not necessarily at the limit of their parental care capabilities during the later stages of nesting. In this sense, Altenburg et al. (1982) found that monogamous birds reduced their parental input, in terms of number of prey items delivered per hour, toward the end of the nestling stage, perhaps indicating that mated males' parental abilities are also "underused" at this time.

A division of sexual roles is usual among birds of prey (Newton 1979) and the presence of both sexes seems essential to successful breeding. However, this division in function becomes blurred in the later stages of reproduction (Newton 1986). As breeding progresses the females contribute gradually more to prey capture and less to other aspects of brood care; sexual roles become similar and can perhaps be undertaken equally by either member of the pair. Role division itself does not necessarily preclude the rearing of nestlings by a single parent, at least in circumstances where the remaining parent is able to increase its investment, as may occasionally occur in some potentially polygynous birds of prey (such as *Circus*; Newton 1976, Cramp and Simmons 1980) when they are breeding monogamously (Altenburg et al. 1982).

RESUMEN.—El macho de un pareja de Aguiluchos laguneros quedó viudo cuando los pollos contaban con 37–38 días de edad. El macho consiguió sacar adelante un pollo intensificando el esfuerzo reproductor y supliendo en parte las funciones realizadas por la hembra: aumentó el número de cebas, el tiempo invertido en el área de cría y las defensas del territorio. Ello parece indicar que al final de la cría los aguiluchos monógamos con polladas escasas no se encuentran al límite de sus posibilidades y que la contribución relativa de cada sexo a los cuidados parentales es susceptible de variar en función de las necesidades familiares de cada momento.

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BATS AS PREY OF STYGIAN OWLS IN SOUTHEASTERN BRAZIL

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Few studies have examined quantitatively large numbers of pellets or stomachs for assessing the relative frequency of bats as prey of owls (cf., Uttendörfer 1943, Ruprecht 1979, Mikkola 1983). Pellets cast by three or four Stygian Owls (*Asio stygius*) were collected during 25 mo, mostly between June 1985 and February 1987 and sporadically in August–September 1989, December 1990 and February 1991. We collected pellets under trees in a *Pinus* sp. plantation located in São Carlos, São Paulo State, southeastern Brazil (21°58'S, 47°52'W) at an altitude of 840 m. The climate of the study area is a transition between Köppen's Cwai and Awi, or rainy tropical with dry (April to September) and wet (October to March) seasons (Tolentino 1967). The nocturnal foraging activities of the owls took place in savannah ("campo cerrado") and grassland ("campo") habitats near the *Pinus* plantation, which was used for diurnal roosting. All data were gathered through direct observation in the study area.

A total of 422 pellets were analyzed after treatment with a 3% boiling solution of NaOH (Schueler 1972). Prey remains were identified by comparison with reference collections. The bulk of the prey items consisted of small birds (Table 1), mostly finches (e.g., *Volatinia jacarina* which alone comprised 62.5% of all birds or 56.3% of all prey), weighing 10–15 g (J.C. Motta Junior unpubl.). Bats were the second most frequent prey whereas insects

Table 1. Numbers of prey items found in pellets of Stygian Owls in two climatic seasons in southeastern Brazil.

	DRY SEASON		WET SEASON		TOTAL	
PREY	*N*	(%)	*N*	(%)	*N*	(%)
Bats	49	(5.7)	26	(6.8)	75	(6.1)
Birds	793	(93.1)	318	(83.7)	1111	(90.2)
Frogs	0		1	(0.3)	1	(0.1)
Insects	10	(1.2)	35	(9.2)	45	(3.6)
Total Prey	852	(100.0)	380	(100.0)	1232	(100.0)
Total Pellets	265		157		422	

Table 2. Bats ($N = 75$) found as prey of Stygian Owls in southeastern Brazil. Body weights were obtained from museum specimens, collected in São Paulo state.

Species	Weight (g) (Range)	(N)	No. (%) of Bats in Pellets
Molossidae			
Eumops glaucinus	28.6–38.6	(12)	47 (62.7%)
Nyctinomops laticaudatus	8.5–13.8	(6)	10 (13.3%)
Nyctinomops macrotis	26.0	(1)	1 (1.3%)
Vespertilionidae			
Eptesicus furinalis	5.0–7.2	(8)	3 (4.0%)
Histiotus velatus	7.0–10.8	(9)	1 (1.3%)
Lasiurus blossevillii	8.7–11.4	(3)	1 (1.3%)
Lasiurus cinereus	14.3–23.5	(3)	3 (4.0%)
Lasiurus ega	14.3–15.0	(3)	6 (8.0%)
Phyllostomidae			
Glossophaga soricina	8.2–12.0	(86)	1 (1.3%)
Chiroderma doriae	26.9–33.0	(18)	1 (1.3%)
Pygoderma bilabiatum	15.4–15.9	(2)	1 (1.3%)

(Scarabaeidae and Orthoptera) and a frog seemed to be of minor importance. The absence of rodents in the diet of the Stygian Owls studied was surprising. Rodents were abundant in the study area as evident from their frequent occurrence in pellets of Barn Owls (*Tyto alba*) living in the same area (Motta Junior 1988).

G-tests (Sokal and Rohlf 1969) applied to seasonal frequencies of prey items (Table 1) demonstrated that insects were more frequently preyed upon during the wet season ($G = 39.92$, $P < 0.001$), whereas consumption of birds and bats did not show seasonal trends ($G = 2.58$, $P >$ 0 10 and $G = 0.35$, $P > 0.50$, respectively).

Eleven species of bats in eight different genera and three families were recorded. The largest bat (*Eumops glaucinus*) was also the most frequently preyed upon by Stygian Owls (Table 2).

Data from Colombia (Borrero 1967), Belize (Franz 1991) and from Colima, Mexico (based on three pellets) were similar to ours. Except for the Black-and-White Owl (*Ciccaba nigrolineata*) that forages heavily on bats (Ibáñez et al. 1983) and the Stygian Owl (this study), apparently no other owls include bats so frequently (6.1%) in their diet (cf., Uttendörfer 1943, Earhart and Johnson 1970, Burton 1973, Mikkola 1983).

RESUMEN.—Durante 25 meses, entre junio de 1985 y febrero de 1991, estudiamos la ocurrencia de murciélagos en la dieta del Tecolote Fusco (*Asio stygius*) en el sudeste de Brasil. El análisis de 422 egagrópilas rindió 1232 presas entre las cuales las aves representaron 90,2%, los murciélagos 6,1%, los insectos 3,6%, y los anuros 0,1%. Identificamos 11 especies de murciélagos entre 75 individuos. *Eumops glaucinus* fue la especie más frecuente (47 individuos). La predación de murciélagos fue regular a lo largo de las estaciones. *Asio stygius* es apuntada como una de las especies de Strigiformes que más preda murciélagos en todo el mundo.

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Food-Stressed Great Horned Owl Kills Adult Goshawk: Exceptional Observation or Community Process?

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Great Horned Owls (*Bubo virginianus*) can prey on other owl and diurnal raptor species up to the size of Northern Goshawks (*Accipiter gentilis*), and the question has been raised why this behavior occurs and whether it affects the structure of raptor communities (Craighead and Craighead 1956, Mikkola 1983, Voous 1988). Most reports originate from analyses of pellets of prey remains collected at owl nests and roost sites. There is little specific information on how the owls kill potential harmful prey, nor about the ecological conditions that facilitate such predation. During our study of avian predation in the boreal forest ecosystem near Kluane Lake in the southwestern Yukon (Krebs et al. 1992), we encountered circumstantial evidence for an owl predation of an adult female goshawk, which led us to a revised assessment of such interspecific killings among raptors.

On 18 June 1991, we found a goshawk nest on the flat top of a dead White Spruce (*Picea glauca*) about 10 m high. The nest was unusually exposed above canopy height of the surrounding trees (all other 28 goshawk nests found in our study areas were 4–8 m below canopy height). Fresh streaks of whitewash and two plucking sites with fresh prey remains indicated that the nest was active, and we were attacked by both parents. Because we heard loud begging calls, but the chicks were not yet visible at the nest edge, we estimated their ages to be 2–3 wk.

On 25 June 1991, the nest area was quiet and there were no fresh whitewash or new prey remains. We found numerous breast feathers and the left wing of an adult goshawk 2 m from the base of the nest tree, together with four Great Horned Owl feathers. More goshawk feathers, including a goshawk's right wing, were found under a 1 m high log perch about 12 m from the nest tree. The wings measured 356 mm, indicating they were from a female goshawk (Mueller and Berger 1968). Because the goshawk remains were several days old on 25 June, we estimated that the predation occurred between 18 and 22 June.

During the same period, we monitored a Great Horned Owl family with a nest 1.0 km from the goshawk nest. The two owl fledglings were tethered to an elevated artificial platform for diet study (Petersen and Keir 1987). We moved two additional young Great Horned Owls to the platform for a brood size manipulation experiment from 10–20 June. The adult female owl was equipped with a backpack radiotransmitter, and we recorded her locations once every second night. Food stress during the brood addition experiment was suggested by a decrease in the amount of food brought to the platform, declining owlet weights, and increased hunting distances from its nest by the female owl. The goshawk nest was within the territory of the owl pair, but the telemetry locations did not reveal any relation to the goshawk nest. On 27 June, we found the remains of the right leg of an adult female goshawk beside the owl tethering platform. The remains were several days old, and presumably were dropped by the owls

Discussion

Why Publish a Single Observation? Because of the nature of rare events, a sufficient sample size for testing hypotheses can only be achieved as a collaborative effort of different researchers who publish few or even single observations on this topic (Schmutz 1992). The fact that Great Horned Owls kill other birds of prey has been well documented (reviews in Craighead and Craighead 1956, Mikkola 1983, Voous 1988), and no further publications are needed to simply report this behavior. We agree with Bortolotti (1992) that the publication of single observations should allow links to the analysis or interpretation in a higher-level context. As a consequence, we suggest not publishing short notes that simply report the interspecific killing among raptors—instead we should ask the question when and why it occurs, and focus on the context of these observations. In our case, we present a single observation with additional information that shows potential links to causes and implications of this behavior: we will 1) try to estimate how rare such events were during our study, and 2) discuss how the documented details of the ecological context of both predator and prey relate to hypotheses on the evolution of interspecific killing among raptors.

How Frequently do Great Horned Owls Kill Other Birds of Prey? We monitored 17 goshawk nests during 1989–91 and found a maximum of two possible cases of Great Horned Owl predation on goshawks. The second case was a brood that disappeared for unknown reasons. The described goshawk nest was exposed above canopy height, which is an unusual situation in our study area and elsewhere (Shuster 1980, Hall 1984). Owl predation may rather affect the nest site selection than the population dynamics and density of other raptors. Predation by Great Horned Owls, however, has been reported to account for higher mortalities in other species: up to 30% of juvenile Spotted Owls (*Strix occidentalis*; Forsman et al. 1984, Gutierrez et al. 1985, Miller and Meslow 1986), 65% of juvenile Great Gray Owls (*S. nebulosa*; Duncan 1987), 0–

44% of young Red-tailed Hawks (*Buteo jamaicensis*; McInvaille and Keith 1974, Houston 1975), up to 27% (Walton and Thelander 1988) or locally even more (Steidl et al. 1991a) of fledged or released Peregrine Falcons (*Falco peregrinus*), up to 21% of hatched Ospreys (*Pandion haliaetus*; Steidl et al. 1991b), 25 predations on young Harris' Hawks from 64 nests (*Parabuteo unicinctus*; Dawson and Mannan 1991). It is possible that the literature is biased toward high predation, because surprising results may be more likely to be published. We encourage also the reporting of low predation rates in areas where the populations of several raptor species are known.

Killing Other Birds of Prey: a Response to Food Stress? We found it interesting that the goshawk was killed by an owl under food stress, which we had induced experimentally. During our study, the overall prey base was high because Snowshoe Hares (*Lepus americanus*) were at the peak of their population cycle (Krebs et al. 1992), and the overall predation by owls on goshawks was low. It is intriguing to hypothesize that top-predators kill lower-level predators more often when other prey is scarce. In support of this hypothesis, McInvaille and Keith (1974) found a lower predation rate by Great Horned Owls on Red-tailed Hawks when Snowshoe Hares were at peak densities. More predation rates on raptors should be reported in conjunction with estimates of other prey species.

Raptors Killing Raptors: Predation or Competition? Observations of raptors killing raptors have been considered anomalies. As a consequence many short notes and specific lists in handbooks have been published (review in Voous 1988). This perspective is based on the assumption that raptors are a costly prey because of the high risk of injury to an attacking predator. Why raptors kill other raptors despite the high costs involved, has been explained by the additional benefits of removing a potential competitor (review in Mikkola 1983). Benefits other than reduced competition for food may be reduced competition for nest sites, increased protection of young from predation, and increased protection from harassment (Klem et al. 1985).

When raptors kill other raptors, do they really suffer a higher risk of injury? We are not aware of analyses of risks involved in capturing different prey. Our case of an owl possibly attacking a brooding or sleeping goshawk suggests that there may be no more risk involved than when attacking any other prey. The most parsimonious explanation is that raptors kill raptors simply to obtain food, or in other words, to obtain direct and immediate benefits. At the present state of our knowledge, we should take this simple explanation as a null-hypothesis, and our scientific effort should be directed toward testing it. We can reject this null-hypothesis only if field data do not meet the predictions derived from it. For example, the null-hypothesis predicts that killed raptors are as likely to be consumed as any other prey, or that the proportion of raptors in the diet should reflect their availability as much as any other prey.

CONCLUSIONS

A Great Horned Owl killing an adult goshawk was a rare event with little impact on the goshawk population during our study. The frequency of such predation may vary with prey abundance, however, and may be more pronounced when other prey is scarce. Based on the detailed knowledge of the ecological situation of our case, we question the current perspective that raptors killing raptors are anomalies that involve a high risk and require competition as an explanation. More observations in a known context are needed to test hypotheses on why this phenomenon occurs.

RESUMEN.—Hemos estudiado los nidos del Gavilán Azor (*Accipiter gentilis*) y del Tecolote Cornudo (*Bubo virginianus*) que estuvieron ubicados a 1 km de distancia el uno del otro. Los residuos encontrados en ambos nidos son evidencia de que uno de los búhos de la especie *B. virginianus* mató a un *A. gentilis* hembra cerca de su nido. Los búhos estuvieron sometidos a escasez de comida, la que fue inducida por nosotros al aumentar el número de pollos en el nido. El nido del *A. gentilis* estuvo extremadamente expuesto. Durante nuestro estudio, esta depredación fue un evento raro, con poco impacto en la población de *A. gentilis*. La frecuencia de tales depredaciones puede ser más numerosa cuando la presa es escasa. Basados en el conocimiento detallado de la situación ecológica de nuestro estudio, nosotros dudamos de la creencia de que la muerte de una ave raptora causada por otra, es una anomalía que lleva un gran riesgo, y que sólo se explica por la competencia entre raptoras.

[Traducción de Eudoxio Paredes-Ruiz]

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NESTING ASSOCIATION BETWEEN THE WOODPIGEON (*Columba palumbus*) AND THE HOBBY (*Falco subbuteo*)

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Nest predation is the main cause of breeding failure in birds (Ricklefs 1969). Various mechanisms for defending nests against predators have evolved. In their classification of nest defenses, Collias and Collias (1984) recognized, among others, species which use "protective nesting association with formidable species"; the formidable species can be large birds of prey, wasps, bees or termites and their nests, or humans and their habitations. It is presumed

that potential predators risk death or serious injury from the dangerous species, if they try to prey on nests of the protection-seeking species. It is usually said that in this kind of symbiosis the species seeking protection do not incur intrinsic costs such as predation or egg and chick loss due to attacks from the associated dangerous species (Collias and Collias 1984).

We describe an association between nesting Woodpigeons and Hobbies. Apart from Bijlsma (1984) there have only been anecdotal descriptions of this phenomenon by various authors, reviewed by Collar (1978) and by Bijlsma (1984). Cain et al. (1982) and Kazakov (1976, in Cramp 1985) have reported the association between Woodpigeons and other raptors.

STUDY AREA AND METHODS

The study was carried out in a 62 km^2 plot bordering the course of the Po River, in northern Italy, where poplar (*Populus* sp. cultivars) plantations predominated. These host a dense population of nesting Hobbies with 25.8–29.0 pairs/100 km^2 and a mean nearest neighbor distance of 1.5 km (SD = 0.7, N = 35). This is one of the highest densities so far recorded (Bogliani 1992). The poplars are mainly from a single clone (I-214) and are therefore genetically identical. They are planted at regular intervals, with 5–6 m between trees.

The Hobby used only Hooded Crow (*Corvus corone cornix*) nests, selecting those in plots with larger trees (circumference at 130 cm greater than 100 cm). Mean hatching date was 18 July, based on 29 nests closely observed from 1985 to 1988.

Observations on breeding biology were carried out from 1985–88. Nests were searched for during July and August by inspecting all abandoned Hooded Crow and Woodpigeon nests. In 1987 the occurrence of both the Hobby and the Woodpigeon was carefully checked in 25 plots (surface of each plot 0.2–1.0 km^2) with poplars of the suitable size. A detailed map, showing each tree, Hooded Crow and Woodpigeon nest within a radius of 100 m from 11 of the 18 Hobby nests found in 18 plots was drawn.

RESULTS AND DISCUSSION

Woodpigeon and Hobby nests were significantly associated in the same plots. Of 17 plots with nesting Woodpigeons, only 1 did not also simultaneously host the Hobby. On the other hand, the Woodpigeon was absent in only 2 of the 18 plots with Hobby nests (Fisher exact test, P = 0.001).

Woodpigeon nests tended to be clumped around a Hobby nest, and in most cases were less than 40 m from the falcon nest (Fig. 1). We found a significant difference between the observed frequency of occurrence in five 20 m distance classes from the Hobby nest, and the expected frequency if the trees in the plot were used at random (χ^2 = 103, df = 4, N = 45, P < 0.001; Fig. 1). The ratio of used vs. available trees was highest in the nearest distance class. The minimum distance was 5 m, the nearest tree to the Hobby nest; there were no cases of simultaneous nesting on the same tree. The 20 to 40 m distance class was also preferred, while over 40 m Woodpigeon nests were less frequent than expected. The average number of Woodpigeon nests present within 100 m of the 11 Hobby nest was 4.1 (SD = 1.8).

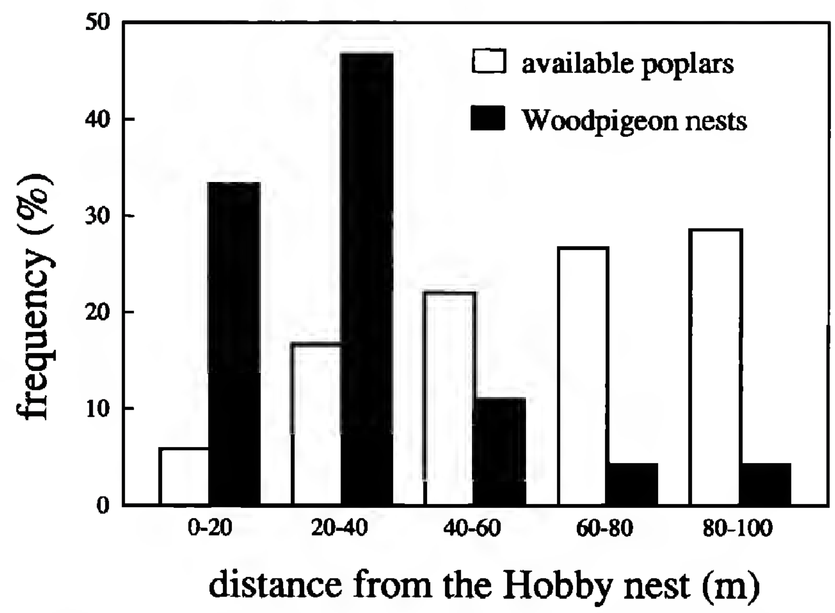

Figure 1. Woodpigeon use of poplars for nesting (N = 45) at varying distances from Hobby nests (N = 11) northern Italy and availability of poplars within the same distance classes (N = 6866).

The Woodpigeon started nest building after Hobbies were settled in their nest and therefore apparently sought the association with the raptor. It appears unlikely that the association was simply due to their sharing the same macro- and micro-habitat requirements. Poplar plantations with large trees suitable for both species were widely available in the study area.

We were unable to identify a preference by the Hobby for certain micro-habitat features such as tree and plantation structure, using univariate and multivariate statistical techniques with a set of 11 variables. The Hobby seemed to choose crow nests only on the basis of the macro-habitat and the need to space out the nests, but was unselective as regards micro-habitat (Bogliani et al. 1992). Trees close to the raptor nests were highly preferred by nest building Woodpigeons. Collar (1978) has suggested that the strong preference by the Woodpigeon for nesting very close to the Hobby may serve to protect the former from nest predators, especially the crows. The Hooded Crow is very common in poplar plantations of our study area, where it reaches very high densities. Crow nest density varies between 14–46 nest per km^2 (Quadrelli 1985). The Woodpigeon is likely to suffer from crow predation, as stated by Tomialojc (1978). The Hobby vigorously attacks all large birds, such as Grey Herons (*Ardea cinerea*) Herring Gulls (*Larus cachinnans*), Black Kites (*Milvus migrans*), Common Buzzards (*Buteo buteo*) and kestrels (*Falco tinnunculus*) which fly within a distance of ca. 50 m of its nest. Hobbies are especially persistent in attacking and driving away Hooded Crows (pers. observation). It may be presumed that Woodpigeons gain the advantage of reduced nest predation if they nest very close to the Hobby, whose attacks keep away crows. The pattern of breeding success of Woodpigeons in the Netherlands was consistent with this prediction (Bijlsma 1984). Although

Woodpigeons expose themselves to the risk of being preyed on by the falcon, this risk is apparently low. As a matter of fact, only two pluckings containing adult Woodpigeon feathers were found on two of the 46 Hobby nests inspected in the study area. It is worth noting that no association seemed to exist between the Woodpigeon and the four Common Buzzard nests found in poplar plantations during this study. Indeed the buzzard commonly preys on Woodpigeons (Cramp 1980, G.B. pers. observation) and therefore the association would be fatal to this latter species.

RESUMEN.—En plantaciones de álamo en el norte de Italia, donde halcones de la especie *Falco subbuteo* anidan con relativamente alta densidad, palomas de la especie *Columba palumbus* construyen sus nidos agrupándoles muy cerca a los de los halcones. Se presume que esta conducta de las palomas reduce la incidencia en la depredación que en sus nidos hacen los cuervos de la especie *Corvus corone cornix*. Estos son fieramente atacados y echados fuera por el *F. subbuteo*. Sin embargo, las palomas adultas corren el riesgo de ser presas de los halcones; residuos de *C. palumbus* han sido hallados entre las plumas de las aves que han sido presas de ellos. Este riesgo, sin embargo, podría ser más alto, en la misma área de estudio, si las palomas anidaran cerca de los nidos de otra especie de raptora, tal como la *Buteo buteo*, que normalmente hace presa de ellas. Esto puede explicar por qué las palomas no se asocian con esa especie.

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LETTERS

BALD EAGLES USE ARTIFICIAL NEST PLATFORM IN FLORIDA

Reports of Bald Eagles (*Haliaeetus leucocephalus*) nesting in human-made nest structures or on artificial platforms are rare. Occasionally, artificial nest structures have been used to replace destroyed natural nests, remove a breeding pair from existing or future human activity, or to promote the expansion of a population (M.V. Stalmaster 1987, The Bald Eagle, Universe Books, NY). Successful acceptance and use of artificial nests by Bald Eagles have been reported from Michigan (S. Postupalsky 1978, Artificial nesting platforms for Ospreys and Bald Eagles. Pages 35–45 *in* S.A Temple [ED.], Endangered birds: management techniques for preserving threatened species, University of Wisconsin Press, Madison, WI) and Arizona (T.G. Grubb 1980, An artificial Bald Eagle nest structure. Research Note RM-383, Forest Service, U.S. Department of Agriculture, Tempe, AZ).

Monitoring of Bald Eagle nesting activities near facilities of Florida Power and Light Company to minimize potential impacts on this endangered species has occurred for more than a decade in Florida (N. Williams-Walls et al. 1986, *Fla. Field Nat.* 14:29–37). In the winter and spring of 1987, a pair of Bald Eagles built a small nest at the intersection of the cross member supports near the top of a 18.3 m-tall power line structure (H-frame) on a 240 kV line southwest of Titusville, Brevard County, Florida. The resident landowner indicated that winds destroyed the nest in 1987. In December 1987 and January 1988, a similar nest was built at the same location; incubation by adult Bald Eagles began in the latter part of January 1988. Much of the nesting material fell to the ground between mid-April and mid-May due to either wind or destruction by the two growing eaglets. Nevertheless, two eagles fledged from this nest.

Late in 1988, a nest was again rebuilt by Bald Eagles at the same location and incubation began in January 1989. Two Bald Eagle chicks hatched in late February 1989 and on 19 April 1989 a wind storm dislodged much of the nest material and both young birds fell to the ground where they died.

In June 1989, we constructed an artificial nesting platform (1.5 m × 1.5 m of 1.9 cm marine plywood attached with five wooden supports to a cross member of the structure) and erected it within 1.5 m of the former nest site. Only minor adjustment in location of the platform was an improvement as the new nest was not directly over a power line and reduced the potential for harm to the birds or interrupted service in the event that wet branches or feces contacted this high voltage line. The platform was painted in a camouflage pattern of green and black and had a series of long slots to facilitate drainage. Also, the upper surface of the platform had about 20 9-cm pegs projecting up and inward to help retain nest material. Vertical structures, sometimes used along sides of the platform to provide protection and/or shade for young, were not placed on this platform.

We built a 1.3-m diameter nest on the platform, with a 50-cm "cup" in the middle, using Loblolly Pine (*Pinus taeda*) branches from nearby trees. Green pine boughs were added to the top to simulate a natural nest. All nesting materials placed on the platform in June 1989 were secured using ropes tied through the slots in the platform. This artificial platform was in place several months in advance of the normal October–April Bald Eagle nesting season in Florida (Stalmaster 1987).

In December 1989, adult Bald Eagles were repeatedly seen perched on or near the artificial platform. Because the nearest pine trees were >100 m away, Loblolly Pine branches and green boughs were placed in two piles on the ground near the power lines. In mid-January 1990, additional sticks were added by the adult Bald Eagles to the nest on the platform. A follow-up investigation indicated that only a small quantity of the nest material provided was used by the adult eagles in completing the nest. Two Bald Eagles chicks hatched and occupied the platform nest until mid-May, when they successfully fledged. This was the first time that Florida Bald Eagles successfully fledged from an artificial nest on an artificial platform. Adult Bald Eagles again used the platform and were incubating in January 1991. Unfortunately, repeated traffic under the nest appeared to disrupt incubation and the platform was abandoned in February 1991.

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GREAT HORNED OWL NESTING IN MONK PARAKEET COLONY IN SUBURBAN CONNECTICUT

The Great Horned Owl (*Bubo virginianus*) is one of the most widespread and successful of North American birds of prey. Throughout its range, it nests in an extremely wide variety of habitats, ranging from desert cacti in the Southwest to forests of the Northeast. Excepting only the Eastern Screech Owl (*Otus asio*), the Great Horned Owl may also be the raptor most tolerant and adaptable to human modified habitats; it has been recorded nesting in a variety of urban and suburban open space habitats, where it usually appropriates nests of crows or squirrels or, less frequently, large cavities in trees (K.H. Voous 1988, Owls of the Northern Hemisphere, The MIT Press, Cambridge, MA).

We report on the nesting of a Great Horned Owl in a Monk Parakeet (*Myiopsitta monachus*) colony in a residential suburb of Bridgeport, Connecticut. This Monk Parakeet colony has existed since the mid-1970s and was, until recently, unique to this site in the state. The colony typically included 90 or more birds and 35–40 active nests at any one time, all constructed in a single ornamental fir (*Abies* sp.) about 19 m tall, in a suburban yard.

The Great Horned Owls used the top of the largest Monk Parakeet nest located along a branch 15.2–15.4 m high. The nest was about 1.8 m in length, 0.6–0.9 m in width and 0.9 m deep. It housed seven pairs of nesting Monk Parakeets, which entered from the bottom or sides. A single Great Horned Owl nestling was first observed in mid-April. It fledged on or about 17 May. Backdating (Anderson and Hickey 1970, *Wilson Bull.* 82:14–28), suggests that the egg deposition was in mid-February and hatching occurred in late March. One adult owl typically roosted in the tree, usually close against the bole and overlooking the nest. The second adult sometimes roosted in a small line of White Pines (*Pinus alba*) about 90 m away. After fledging, both young and adult continued to roost in the nest site tree, always close to the trunk and well within the canopy at heights of 15.2–18.3 m.

Pellets and prey fragments collected from beneath the nest site tree yielded the remains of 22 prey individuals belonging to four species. Of these, 17 (77.3%) were the Norway Rat (*Rattus norvegicus*), 1 (4.5%) an Eastern Cottontail (*Sylvilagus floridanus*) and 2 (9.1%) each were of Eastern Chipmunk (*Tamias striatus*) and Gray Squirrel (*Sciurus carolinensis*). Observations indicated that the Great Horned Owls were taking Norway rats from a small estuary located about 0.5 kilometers from the nest site. The other prey species suggest that the adult owls also sometimes foraged along the lawns.

Although several piles of Monk Parakeet feathers were found beneath the nest site none were found in pellets. However, we did observe the nestling scurrying along a branch toward a parakeet that had landed about 1.5 m away while the adult female watched. Neither it nor the nearby adult were able to capture the parakeet, which flew off as the juvenile owl approached.—**Arnold Devine, Connecticut Department of Environmental Protection, Hartford, CT 06510; Dwight G. Smith, Biology Department, Southern Connecticut State University, New Haven, CT 06515.**

J Raptor Res. 26(4):267–268

RENESTING OF MEXICAN SPOTTED OWL IN SOUTHERN NEW MEXICO

Renesting in the wild by Mexican Spotted Owls (*Strix occidentalis lucida*) has not been documented previously. E.D. Forsman et al. (1984, *Wildl. Monogr.* 87:33) stated that a captive Spotted Owl laid two sets of eggs in two different years, but they made no mention of this occurring in the wild.

We report renesting of a pair of Mexican Spotted Owls in the Lincoln National Forest in southern New Mexico. This pair was included in a study of four mated pairs and one female of a mated pair that were fitted with back-pack radiotransmitters in October 1990. Monitored pairs began roosting together in February 1991 and began nesting in March.

We visited the nest sites at least twice per week to check for young after females were thought to be with eggs. On 3 and 4 May, a single, approximately 10 cm tall owlet was dead at the base of the nest tree of one of the pairs. The

owlet was about 1 wk old. Backdating from the date when this owlet was found, the first clutch of this female was laid during the last week of March or the first week of April. After the owlet died, the female remained on the nest until 20 May. She was also observed roosting within 1–200 m of the male in the vicinity of the original nest on 10, 12, and 19 May.

On 26 May, the female which had lost her young was sitting on another nest in a tree about 100 m farther up the canyon than the first nest tree. During daylight hours on 6 July, she was partially erect on the edge of the nest in a position that was clearly visible from the ground. Prior to this date, it had been difficult to see the incubating female from ground level. Based on her more vertical position on the nest we think that the second clutch of egg(s) hatched immediately before 6 July. On 13 July, an owlet was on the edge of the nest. On 16 July, the partially eaten remains of the female and an owlet were on the ground near the nest tree. Entrails had been removed from the female. A foot was all that remained of the owlet on the ground. Within the nest, we found a portion of the owlet's beak and the female's wing.—**K.W. Kroel and P.J. Zwank, U.S. Fish and Wildlife Service, New Mexico Cooperative Fish and Wildlife Research Unit, New Mexico State University, Las Cruces, NM 88003.**

J. Raptor Res. 26(4):268

American Kestrel Completes Clutch Following Movement of Its Nest Box

Compared with many other raptors, American Kestrels (*Falco sparverius*) are quite tolerant of disturbance during incubation (P.H. Bloom and S.J. Hawks 1983, *Raptor Res.* 17:9–14; T.J. Wilmers et al. 1985, *N. Am. Bird Bander* 10:6–8). Even so, daily disturbance usually causes nest desertion (J.A. Gessaman and P.R. Findell 1979, *Comp Biochem. Physiol.* 63A:57–62). The contents of kestrel nests have been removed and placed in metabolism chambers during incubation (Gessaman and Findell 1979), but I am not aware of any published reports where kestrels continued to incubate eggs that had been moved to a different location. Here I report such an event.

The nest box was initially located in a dead maple (*Acer* sp.) 3 m above the ground in southwest Wood County, Ohio. On 3 May 1992, the nest box, containing two eggs (R. Wensick pers. comm.), was removed from the tree and placed upright on the ground 3 m away. The tree was then felled and cut into pieces. I learned about the situation on 5 May and checked the box at 1205 H, discovering the male incubating four eggs. At 1435 H that same afternoon, the female was incubating the eggs. Fearing that the nest would succumb to mammalian predation if left on the ground, at 1515 H I secured the box to a steel fence post 1 m above the ground and 10 m from where the nest tree had been. At the time, the female was perched on a utility wire 100 m away. At 1620 H, I observed the nest box from a distance of 0.5 km with a spotting scope. The female was then perched on a utility wire 10 m away. At 1628 H, she flew to the box, hovered at the entrance for several seconds, then flew to the cut up nest tree and circled around the pieces of the tree for 2 min. At 1630 H, she flew to the box and entered it. She was still in the box when I left 15 min later. During the evening of 5 May the remains of the nest tree were removed and the stump burned. I observed the nest from 1122–1142 H at a distance of 0.5 km on 6 May. I noticed no activity in the vicinity of the box, but observed a pair of kestrels copulating near a nest box located 1 km to the east, suggesting that the pair had deserted and moved to a new nest site. The translocated nest box contained five cold eggs when checked at 1050 H on 10 May. The pair was again observed 1 km to the east.

Thus, after the nest tree was felled, three eggs were laid: two while the box was on the ground and one after it was placed on the fence post. Incubation was observed, and probably initiated, while the box lay on the ground. Incubation normally commences when the fourth egg is laid in a five egg clutch (R.D. Porter and S.I. Wiemeyer 1972, *Condor* 74:46–53).

These observations show that this pair of kestrels continued to use their nest after it was relocated a short distance away at a lower height. This suggests that kestrel nests may be successfully relocated, if disturbance can be kept to a minimum following relocation.

I thank Richard Wensick for providing the fence post and other materials needed to elevate the nest box, for alerting me that the nest tree had been removed, and for providing information on the date and nest contents when the tree was felled. This, and other nest boxes, were constructed using funds provided by a Paul A. Stewart Award from the Inland Bird Banding Association.—**Thomas W. Carpenter, Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403-0212.**

J. Raptor Res. 26(4):269

AERIAL MOBBING OF A GYRFALCON BY GLAUCOUS GULLS

On 1–2 June 1990, while camped at a small island in Alexandra Fiord on Ellesmere Island (78°54'N 75°45'W) near a lowland oasis (B. Freedman and J. Svoboda 1982, *Can. Field.-Nat.* 96:56–60), I observed a male Gyrfalcon (*Falco rusticolus*) quartering back and forth in front of a cliff where the female was nesting. The orographic lift of the Gyrfalcon was interrupted by a group of three Glaucous Gulls (*Larus hyperboreus*) on two separate occasions, each lasting several minutes. During the first encounter, the gulls, which initiated the engagement, acted in unison, each gull taking turns diving at the Gyrfalcon, while the others circled close by calling loudly. The Gyrfalcon, in an attempt to fight the gulls, swiveled about, talons extended, occasionally even doing so while completely inverted. After returning to the nest, the Gyrfalcon ignored the gulls until after 10 min it tried to make a kill of a single passing bird. The panicked avoidance by the Glaucous Gull consisted of dropping vertically to several meters above the pack ice and calling loudly. Within a few moments, two gulls arrived and the three dissuaded the Gyrfalcon from hunting. The falcon then returned to the nest site where it stayed for the next hour of observation, disregarding nearby gulls.

Gyrfalcons commonly take prey in the air (e.g., C.M. White and R.B. Weiden 1966, *Condor* 68:517–519; S.A. Bengtson 1971, *Ibis* 113:468–476) and customarily prey upon seabirds (e.g., G.P. Dementiev and N.N. Gortchakovskaya 1945, *Ibis* 87:559–565; K.G. Poole and G.A. Boag 1988, *Can. J. Zool.* 66:334–344) including Glaucous Gulls (C.M. White and T.J. Cade 1971, *Living Bird* 10:107–150). Similar mobbing of Gyrfalcons by Common Raven (*Corvus corax*) has been noted previously (M.A. Jenkins 1978, *Auk* 95:122–127). N. Wooden (1980, *Raptor Res.* 14:97–124) also observed perched Gyrfalcons struck by passing Arctic Terns (*Sterna paradisaea*) which, however, never grouped to drive the raptor away as in the present encounter with the larger Glaucous Gulls. This seemingly paradoxical behavior of self-endangerment by mobbers may be necessary to "convince" the predator that their threat is real (S.A. Sordahl 1990, *Wilson Bull.* 102:349–353). The result is that both ravens (Jenkins 1978) and Glaucous Gulls (this study) can be ignored even when they fly directly beneath or over an occupied Gyrfalcon eyrie.—**R.L. France, Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, PQ, Canada H3A 1B1.**

J Raptor Res. 26(4):269–270

AN AGGRESSIVE INTERACTION BETWEEN A NORTHERN GOSHAWK AND A RED-TAILED HAWK

During September 1987, D. Crannell observed an aggressive encounter between a Northern Goshawk (*Accipiter gentilis*) and a Red-tailed Hawk (*Buteo jamaicensis*) on the Alsea Ranger District (Township 13 South, Range 09 West) of the Siuslaw National Forest in the Coast Range of western Oregon. An adult Red-tailed Hawk was observed flying erratically, apparently grappling with another bird. The birds tumbled to the ground a short distance away and when this location was approached, the Red-tailed Hawk was seen hanging upside down in the talons of a mature goshawk about 3 m up in a small tree. The pair of birds were about 5 m from the observer. The goshawk dropped the Red-tailed Hawk, possibly because of the close proximity of a human, and after about 60 sec the Red-tailed Hawk hopped to an adjacent bush. The two hawks then watched each other for a few seconds, and the Red-tailed Hawk flew south across a pasture and landed in a tree. Within seconds, the goshawk pursued the redtail, struck it, and both birds went to the ground. The outcome of this last encounter was not observed.

Vegetation in the area was dominated by second-growth Douglas-fir (*Pseudotsuga menziesii*), vine maple (*Acer circinatum*) and red alder (*Alnus rubra*) growing where recent timber harvest had taken place. This habitat was not typical of most nesting sites for Northern Goshawks in Oregon, and goshawks are not known to nest in the Coast Range of Oregon (R.T. Reynolds et al. 1982, *J. Wildlife Manage.* 46:124–138), although sightings of goshawks are often recorded there. Red-tailed Hawks do nest in the Coast Range. No vocalizations were heard, so it was not known if either bird emitted alarm or defensive calls. It is possible that this encounter was an act of predation by the goshawk on the redtail rather than aggressive territoriality. We do not know if the goshawk consumed any of the redtail. Encounters between Northern Goshawks and Red-tailed Hawks are of interest because of the possibility that the two species are being drawn into closer proximity during nesting because of wide-spread alteration of forested habitat due to timber harvest (D.C. Crocker-Bedford 1990, *Wildl. Soc. Bull.* 18:262–269). Physically aggressive encounters between

two species of similar size are seldom observed, and may be rare in nature, but such direct sources of mortality or competition undoubtedly occur in the wild.

We thank E.C. Meslow, D.K. Rosenberg, and B. Woodbridge for reviewing this note.—**Dan Crannell, Bureau of Land Management, P.O. Box 10226, Eugene, OR 97440-2226; Stephen DeStefano, Oregon Cooperative Wildlife Research Unit, Nash 104, Oregon State University, Corvallis, OR 97331-3803.**

J. Raptor Res. 26(4):270

THESIS ABSTRACT

HABITAT USE, MOVEMENTS, MIGRATION PATTERNS, AND SURVIVAL RATES OF SUBADULT BALD EAGLES IN NORTHERN FLORIDA

The state of Florida supports over half of the breeding population of Bald Eagles (*Haliaeetus leucocephalus leucocephalus*) in the southeastern United States; this represents a significant resource for the Southeast and for Florida. Currently, primary management emphasis and protection is focused on bald eagle nest sites. No habitat protection or management activities are aimed at foraging, roosting or loafing areas for subadult eagles. In fact, habitats and habitat characteristics important to subadults have not been quantified. In this study, I examined various aspects of eagle biology that might be pertinent to survival or management of the Florida subadult eagle population. Specifically, using radiotelemetry, I examined post-fledging habitat needs, factors affecting timing of migration, local movements, habitat use, and survival in north-central Florida from spring 1987 through spring 1991.

Fledgling eagles (birds prior to their initial migration) remained dependent on adults and remained within 4 km of the natal nest until they initiated migration (approximately 7 wk post-fledging). It was determined that habitat protection within the 229 m primary protection zone used in Florida was not sufficient to meet the habitat needs of fledgling eagles and that the protection period should extend until fledglings initiate migration in the summer. Timing of migration for fledgling and 1- to 4-year-old eagles appeared to be correlated more with prey availability than with temperature, although both factors appear to affect migration.

Locations of radio-tagged eagles outside of Florida ranged from South Carolina to Prince Edward Island, Canada. Data suggest that eagles are philopatric to summering areas, which emphasizes the need for protection of significant summering areas. Known and assumed mortality occurred primarily during migration in northern states. The 1½ year age class had the lowest survival. Survival was significantly lower for eagles fledged from 1-chick nests and for the younger chick in 2-chick nests. The minimum survival rate through 4½ years of age was 50% and did not vary by sex.

After subadults returned to the north-central Florida study area in the fall, individuals continued to use the same general areas each year. Temporally and locally abundant food sources resulted in temporary small concentrations of eagles. Certain portions of the study area were used consistently each year by large numbers of eagles. Subadult eagles were not distributed randomly over the study area. Logistic regression analyses revealed that eagles tended to be located close to large water bodies, and eagle nests were frequently in cypress and marsh habitats, and avoided main roads and developed areas. Immature eagles (1-year olds) tended to be located closer to eagle nests than 2- to 4-year-olds Thus, management for subadult populations must include these heavily used concentration areas that supply the habitat features preferred by subadults. Survival of subadults may be affected if a highly used area becomes unsuitable.—**Petra Bohall Wood. 1992. Ph.D. thesis, Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611. Present address: West Virginia Coop. Fish and Wildlife Research Unit, West Virginia University, P.O. Box 6125, Morgantown, WV 26506-6125.**

J. Raptor Res. 26(4):271-273

News and Reviews

Trends in European Goshawks (*Accipiter gentilis*): an overview by R.G. Bijlsma. 1991. *Bird Census News.* Vol. 4:3-47.

The goshawk (*Accipiter gentilis*) is a large, forest-nesting raptor found across the northern hemisphere. This species occurs year-round in a wide variety of habitats in Europe, including forests, woodlands, agricultural and rural-residential areas. These habitats are subject to a diversity of land uses and environmental fluctuations. As the author indicates, the study of goshawk population trends can provide information on local environmental conditions, such as loss of habitat, environmental pollution, human persecution, or declines in other species (goshawk prey). The objective of this article was to indicate trends of breeding goshawks in Europe.

Goshawk population data from 25 countries was examined (Germany is divided into 8 areas, for a total of 32 areas). A discussion and supporting figures are presented for each country, including study area size, goshawk density estimates and environmental factors influencing trends when available from each literature source. Current goshawk population numbers for each country is estimated. The author's summary of population trends by country is displayed in tabular format, for the time period between 1950-90.

This article is an impressive review of literature on the European Goshawk covering population information and environmental threats. Overall, the conclusions of this article appear well supported by references spanning 40 yr. The reader must have faith in the author's interpretive abilities as not all the materials necessary for critical analysis are provided.

The sources referenced are published articles covering a range of study areas, habitats, methodologies and study objectives. Thus, a comparison of nesting densities among studies is not possible. The author's approach is to examine trends in individual populations, and to bring together all available information to make conclusions regarding trends over larger areas. The author admits that this task has its challenges. For example, information on changes in habitat or land use over the length of the study was not always provided by each source. In addition, systematic survey and experienced observers may not have been used in all cases.

The reader might find it difficult to assess the reliability of each source from this article. The original study objectives and methodologies are not presented in all cases, and these original references are not likely to be available to most non-European readers. The author periodically lends his professional judgment as to whether the cited findings were realistic with respect to population trends.

The discussion for each country is supported by a graph of goshawk population trends. The graphs are not always well labeled with country names. Units of measure are used inconsistently in graphs and text to describe goshawk densities and study area size, which makes reading challenging. I would have appreciated the inclusion of a map of the continent depicting countries and study locations.

The author summarizes environmental factors which were cited as affecting European Goshawk populations for three periods over the total 40-year span. Factors mentioned include pesticides, human persecution of goshawks, and changes in habitat and prey availability.

Data available from the period prior to 1955 suggest a slight to strong increase in goshawk populations, possibly a response to prohibition of persecution. In northern Europe, goshawk trends during this period appear to have been to a large extent a response to tetraonid population cycles. The use of persistent pesticides is cited as the cause of dramatic declines in goshawk populations throughout Europe, during the period between 1956-70. This trend was also seen in other bird-eating raptors. The impacts of hunting or persecution on goshawks are difficult to assess but are believed by some to have caused local declines and extinctions during this period. In most European countries the use of persistent pesticides was discontinued by the early 1970s, and goshawk population trends throughout the continent during this period are strongly positive. Densities in western Europe often appeared to peak in the 1980s followed by a decline and stabilization at a lower population level.

Changes in habitat are cited in relatively few sources as causing goshawk declines and cited in fewer cases as resulting in increases. A reduction in forested habitats was due to various causes, which included acid rain, clear-cutting, the use of "modern forestry" practices, forest fires, and conversion of forests to non-native plantations. The maturing of forests and habitat diversification was cited at the potential cause of recent goshawk population increases for one study.

Fluctuation in prey populations was cited as a factor in goshawk population trends. In the boreal forest of northern Europe, cyclic trends in food availability were considered to cause similarly cyclic trends in goshawk numbers. In one reference, adverse forestry practices were believed to be the cause of prey population declines, especially forest tetraonids,

which in turn were believed to cause declines in goshawk numbers. Agricultural and other rural land practices were also suspected causes of depleted prey resources.

The conclusion of the review is that without further large changes in habitat, food supply, or persecution, European Goshawk populations should remain stable in the future. A summary of research over the past 10 yr suggests that 19% of the countries or areas under consideration have goshawk populations that exhibit at least a probable decreasing trend. Forty percent of the areas have goshawk populations that are suspected to be stable or increasing. The remaining areas have goshawk populations which appear to exhibit variable trends (16%) or have populations for which no reliable information exists (25%). The primary contribution of this article may be to focus attention on European Goshawk populations that appear to be declining or for which little is known.—**Karen K. Austin**

The International Osprey Foundation (TIOF) is seeking applications for its fourth grant to support research activities of a graduate student primarily focusing on ospreys. Work with other raptor species may be considered, however. The award recipient will be expected to provide a report on his or her research and use of the funds within a year of receiving the grant.

Applicants should submit a proposal outlining their project and the intended use of the funds by December 31, 1992. The grant will be awarded on March 31, 1993. Please send a project description of no more than two pages. Also provide an itemized estimate of expenses and the name, address and phone number of the graduate supervisor. Send applications to: **TIOF, Endowment Fund, P.O. Box 250, Sanibel, FL 33957-0250.**

MANUSCRIPT REFEREES

The following persons kindly volunteered their insight and spent valuable time in reviewing manuscripts for the *Journal*: Dean Amadon, James G. Auburn, Thomas G. Balgooyen, Samuel J. Barry, Marc J. Bechard, James C. Bednarz, Daniel D. Berger, John Bielefeldt, Robert G. Bijlsma, Keith L. Bildstein, Peter H. Bloom, David A. Boag, Gary R. Bortolotti, Thomas Bosakowski, William W. Bowerman, Richard D. Brown, Mitchell A. Byrd, Tom J. Cade, Thomas W. Carpenter, Paul M. Cavanagh, Richard J. Clark, William S. Clark, Jack Clinton-Eitnear, Patrick Colgan, Charles T. Collins, Michael W. Collopy, A. R. Craig, John L. Curnutt, Dale W. Stahlecker, Martha Desmond, Stephen DeStefano, José A. Donazar, Gary E. Duke, Jame R. Duncan, David H. Ellis, John T. Emlen Jr., James H. Enderson, Dave L. Evans, Roger M. Evans, Peter Ewins, Fran Hamerstrom, John R. Faaborg, Jim Fitzpatrick, Stephen P. Flemming, Dale E. Gawlik, Laurie Goodrich, Daniel N. Gossett, Jon S. Greenlaw, Curtice Griffin, Lucinda Haggas, Alan H. Harmata, Judy Henckel, Charles J. Henny, Fernando Hiraldo, Anne Hoag Wheeler, Stephen W. Hoffman, Denver W. Holt, C. Stuart Houston, Richard Howard, Grainger W. Hunt, William M. Iko, Eduardo E Iñigo-Elias, Chris Iverson, Fabian M. Jaksić, Paul C. James, Jamie E. Jiménez, Enrique R. Justo, Richard H. Kerbes, Paul Kerlinger, Mark Kopeny, Jeff Lincer, Douglas MacCoy, Santi Mañosa, Mark S. Martell, Carl D Marti, Kathy Martin, John M. Marzluff, Katherine McKeever, Brian A. Millsap, Douglas W. Mock, Martin L. Morton, Charles A. Munn, Robert K. Murphy, Robert W. Nero, R. R. (Butch) Olendorff, Jim W. Parker, Jimmie Parrish, James R. Philips, Howard R. Postovit, Patrick T. Redig, Marco Restani, Richard T. Reynolds, Robert J Ritchie, Ricardo Rodríguez-Estrella, Christoph Rohner, Robert N. Rosenfield, David A. Ross, J. Stan Rowe, William C. Scharf, Wolfgang Scherzinger, Peter E. Scott, Steve Sherrod, Williston Shor, Dwight G. Smith, Noel Snyder, Mark Stalmaster, Paul F. Steblein, Karen Steenhof, Ernst Sutter, Ted Swem, Ethan J. Temeles, Jean-Marc Thiollay, Paddy Thompson, Sergio Tiranti, Philip L. Trefry, Dan Varland, Ian G. Warkentin, James W. Watson, Clayton M. White, Karen L. Wiebe, Edwin O. Willis, Neil D. Woffinden, Petra Bohall Wood, Fridjof Ziesemer, Dale Zimmerman, Fred C. Zwickel.

NEWS

1991 STEPHEN R. TULLY MEMORIAL GRANT RECIPIENTS

Keith J. Merkel

Keith J. Merkel is a native and resident of Marshfield, Wisconsin, where he is employed as a Quality Control Supervisor in a manufactured housing production facility. He is an active outdoorsman who enjoys backpacking, canoeing/kayaking, travel, and photography. He also is an avid amateur ornithologist and bander, with a special interest in raptors. Currently he is researching the diet, breeding habitat, nesting success, range, and distribution of several raptor species in central and northern Wisconsin. As part of these long term studies he has installed over 100 nest boxes and platforms for American Kestrel and Eastern Screech, Northern Saw-whet, Barred, and Great Gray owls. Annual visits to these nesting structures yield data on clutch size, brood size, prey species, fledgling success rates, fledgling dispersal, and nest site fidelity. In 1988 Wisconsin's first documented nesting Great Gray Owls successfully fledged four young from one of these platforms, establishing that this species does, at least occasionally, breed in the state.

Neal D. Niemuth

Neal D. Niemuth was born and raised in Stetsonville, Wisconsin, where his early raptor experience involved erecting kestrel nest boxes and climbing for local banders. After earning a Bachelor of Science degree in English from the University of Wisconsin at Stevens Point, Neal taught high school for five years before beginning work on a Master of Science degree in zoology at the University of Wyoming. For his thesis Neal is testing the role of nest predation in Sage Grouse lek formation, as well as the effect of nest density on predation of Sage Grouse nests.

In addition to his Sage Grouse study, Neal continues to work with raptors. He is currently studying natal dispersal of Osprey, philopatry and productivity of kestrels, and population ecology of Saw-whet Owls in northern Wisconsin.

CONTENTS FOR VOLUME 26, 1992

NUMBER 1

NUMBER 2

Number 3

[1]This issue was jointly edited by Josef K. Schmutz and Keith L. Bildstein. Artwork was kindly provided by Deann L. De La Ronde, Mónica Herzig and Jonathan Wilde.

NUMBER 4

The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, letters to the editor, thesis abstracts and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 215 by 280 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. Submit the current address on a separate page placed after the literature cited section. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (6th ed., 1983) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1990).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 24(1–2), which is available from the editor.

1993 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1993 annual meeting will be held on 3–7 November at the Marriott City Center Hotel in Charlotte, North Carolina. Details about the meeting and a call for papers will be mailed to Foundation members in the summer, and can be obtained from Keith Bildstein or Laurie Goodrich, Scientific Program Chairpersons, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A., Voice (215) 756-6961, FAX (215) 756-4468. For further information about the meeting or the associated symposium "Raptors Adapting to Human Environment" and art show, contact Robert Gefaell, Local Committee Chairperson, P.O. Box 16443, Charlotte, NC 28297 U.S.A., Tel. (704) 334-8078 or (704) 875-6521 (Carolina Raptor Center).

RAPTOR RESEARCH REPORTS

#1, R.R. Olendorff. 1971. *Falconiform Reproduction: A Review Part 1. The Pre-nestling Period.* $10.00 members, $12.50 non-members.

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#7, R.R. Olendorff [Editor]. 1989. *The Raptor Research Foundation, Inc. Bibliographic Index (1967–1986)*. $2.50 members, $5.00 non-members.

#8, R.R. Olendorff, D.D. Bibles, M.T. Dean, J.R. Haugh and M.N. Kochert. 1989. *Raptor Habitat Management under the U.S. Bureau of Land Management Multiple-Use Mandate.* $5.00 members, $6.50 non-members.

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BOOKS

Biology and Management of Bald Eagles and Ospreys. Proceedings of the First International Symposium, Montreal, Canada.
D.M. Bird [Editor]. 1983.
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